Thesis

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Implications and management of *L. salmonis* in Norwegian aquaculture

A literature review

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Introduction:

Thesis introduction

The continental coastline of Norway is approximately 3000 km long, characterized by its many islands and fjords. The gulf stream transports warm water from the Gulf of Mexico to the north Atlantic, ensuring year-round ice-free waters and optimal temperatures. Water quality and geographical conditions are considered ideal for rearing Atlantic salmon (*Salmo salar)* and Rainbow trout (*oncorhyncus mykiss*). The networks of deep fjords provide shelter from rough seas and river run-off creates a brackish top water layer in the fjords favourable for salmonids. (Jones and Beamish, 2011, pp. 31–34)

The first fish farms in Norway were established as small scale family businesses in the 1950s, and the industry has since grown to be among the nations' most important export trade good. In 2018 the yearly production of fish for food equalled 1.35 million tonnes, with a net value of 6,4 billion euro ("Statistisk sentralbyrå, akvakultur," 2018). The aquaculture industry is also essential in providing workplaces and contribute to the persistence of settlements along the coastal districts of Norway. The main farmed species are Atlantic salmon and rainbow trout, but as a result of salmon louse management, the production of cleaner fish has recently emerged as a major aquaculture product as well (Jones and Beamish, 2011, p. 153; Powell et al., 2018).

A noticeable increase in infestation by *L. salmonis* was first documented in Norway on wild and farmed salmonids in the early 90s (Jones and Beamish, 2011, pp. 281–283). Premature return to rivers and estuaries of sea trout was recorded together with significant skin pathology and emaciation, coinciding with areas of intensive farming activity (Thomassen et al., n.d.). Several studies suggest that the intense farming of susceptible host populations is to blame for the increasing levels of infestation. The open net cages provide continuous access to large numbers of salmonids, resulting in constant re-infection and massive shedding of infectious larvae to the environment. (Tully et al., 1999).

The industry spent approximately 520 million euro in the direct management of salmon louse in 2018, but infestations represents not only an economical problem; the increasing presence of lice is currently the biggest threat towards environmental sustainability in Norwegian aquaculture, causing pressure on both wild fish stocks and other marine organisms. Sustainability is the most important prerequisite for the persistence and development of the industry, which is why so much attention and resources have been invested in the management of the salmon lice. The Norwegian Aquaculture Act is a collection of national laws from 2006. It's purpose is stated as "to promote the profitability and competitiveness of the aquaculture industry within the framework of a sustainable development and contribute to the creation of value on the coast." ("akvakulturloven - Lovdata," 2006; Olsen, 2019)

The goal of this thesis will be to collect, organize and recapitulate the large amount of information available on the topic of *L. salmonis* into a systematic overview, describing its significance in Norwegian aquaculture, aspects of management and future challenges. Recent findings and studies will be put into context with already known information and provide the reader with a progressive understanding of the present status and implications of the ectoparasite, *Lepeophtheirus salmonis*, in Norwegian aquaculture.

Material and methods

There is a large body of scholarly sources available on the topic of *l. salmonis*. A simple search for "Lepeophtheirus salmonis" on Google Scholar yields 7,770 hits, while "salmon lice" yields 24,000. In order to reduce the list to more relevant information, keywords applicable to the defined topic in question have been added. I have also used the library of the Veterinary University in Oslo and its database for collecting relevant literature. Reports and public information available from national monitoring programs have been particularly useful in providing an overview of both the development and present status of the subject matter.

I also spent one month in practice at an accredited fish health service company in northern Norway (Marin Helse^{as}) to help acquire a realistic picture of the challenges and practical implications of *L. salmonis* in field. This experience was useful when constructing the concept and framework of my thesis.

Salmon lice biology and ecology

L. salmonis is a common and widespread marine ectoparasite occurring in all cold, temperate waters of the northern hemisphere. The louse belongs to the crustaceous Caligidae family, a group of parasitic copepods known as sea lice. There are two main species of sea lice relevant to the Norwegian aquaculture; *Lepeophtheirus salmonis* and *Caligus elongatus*. *C. elongatus'* prevalence patterns have until recently shown moderately low and steady levels, and not much scientific attention or resources have been dedicated to it as of yet. (Jones and Beamish, 2011)

Lepeophtheirus salmonis has long been regarded as the most important species of sea lice due to its significant impact on the Norwegian aquaculture and wild fish stocks. It will therefore be the topic of this literature review.

Host susceptibility

Lepeophtheirus salmonis is considered a stenoxenous parasite, specific to only salmonids. In 2006, the presence of non-egg carrying individuals was documented on the three-boned stickleback, but no evidence of full life cycle completion has been found, suggesting it may only serve as a potential intermediate host. Egg carrying females have been identified on Sea bass and Saithe, but as all these individuals were collected in proximity to aquaculture farms it is not known if the lice were transferred from known susceptible species post-maturation. (Jones and Beamish, 2011, pp. 15–17).

A study was performed on three different salmonid species (Atlantic salmon, rainbow trout and Coho salmon), revealing individual difference within the susceptible species. *L. salmonis* was found to mature the slowest on the Coho salmon, followed by the Rainbow trout. The quickest maturation was recorded on Atlantic salmon, which also had higher average abundance of lice than the rainbow trout. No significant differences could be identified in the blood physiology of any of the fish species, indicating the relevant differences lie in the fish' epithelium and mucus. (Fast et al., 2002)

Fast et al. also found that the lice' production of proteases and alkaline phosphatases differed in response to the different species mucus. In less susceptible species such as the Pacific Silver salmon, louse secretion of trypsin and Prostaglandin E was found to be considerably less prominent. The less susceptible species also demonstrated a stronger tissue response to the parasite presence.(Fast et al., 2002)

Life history of *L. salmonis*

The life history of *L. salmonis* should be put in context with its coexistence with the wild salmonids and their anadromous, migratory behaviour pattern. Only during juvenile migration from rivers and when the spawning adults return, are the conditions (high stocking density and ocean salinity) favourable for the infestation and proliferation of *L. salmonis*. In between the salmon migration periods, the coast-residential trout is believed to support the coastal presence of over-wintering lice (Penston and Davies, 2009). The life expectancy of the louse has been recorded as up to 210 days under laboratory conditions, suggesting its capability of surviving the winter and returning to the coastal origins with the spawn-ready salmon. (Mustafa et Al).

This natural limitation in seasonal host accessibility has probably historically ensured a sustainable balance in the host-parasite relationship. However, with the year-around high stocking of open net pens, the reproductive and infestation potential stay continuously high, supporting a large abundance of lice and shedding of infectious larvae (Jones and Beamish, 2011).

Salinity tolerance

Salinity is a major influencer of sea louse population dynamics. The salinities of which *L. salmonis* is exposed to may vary greatly throughout its life. Salmonids are found in both the low-salinity waters of brackish fjords and river mouths as well as the open oceans during their migration, and the attached louse will experience a salinity identical to that of the host unless they detach. By consuming host mucous and blood, the attached lice-stages may survive a week or more at salinities down to 7 ppt (parts per thousand). The eggs, however, will not survive freshwater exposure and in laboratory conditions no hatching was found to occur below 20 ppt. Planktonic stage mortality occurs at around 15 ppt salinity, and infectious copepods will aggregate close to haloclines near river mounds in order to increase the chance of encountering migrating host species. (Groner et al., 2019).

This information may help explain the early returning wild salmonids observed since the early 1990s as Wild Sea trout is known to seek freshwater in order to self-control sea lice infestations (Wagner et al., 2008). They have been reported to remain in freshwater for more than a month, at the cost of reduced growth and increased mortality. (Groner et al., 2019)

Reproductive features

L. salmonis' life cycle is direct, meaning it is dependant only on a single host to reproduce. However, more hosts may be involved; during the mobile phases (pre-adult and adult) the salmon louse is able to detach from its current host and transfer to new individuals with relatively high success, 63% and 52% for male and female lice respectively, over a period of 4 days (Jones and Beamish, 2011; Ritchie, 1997).

The iteroparous female has a very high reproductive capability, with the potential of producing up to 11 successive pairs of egg strings during her lifetime. Each string may contain up to 1000 viable eggs on wild hosts (Mennerat et al., 2017) Number of eggs per egg-string is highly variable, and influenced by different factors such as temperature, host species, farmed versus wild fish and potential exposure to drugs. (Jones and Beamish, 2011, pp. 2–7). The adult female hatches her eggs directly into the water column starting from the distal end of the egg string in sequence.

The generation time of *L. salmonis* has been observed to significantly correspond with the water temperature. The average generation time at 6ºC was 8-9 weeks, while at 18ºC it was significantly shorter at only 4 weeks. The time for hatching has been found to vary from 17,5 days at 5ºC to 5,5 days at 15ºC (Jones and Beamish, 2011, p. 4). A study was recently performed on more extreme temperatures. It was found that the fastest development time to adult stage without increased mortality was 21ºC. At 3ºC (the lowest temperature tested) very few males and females developed into full adults. (Hamre et al., 2019)

Louse development

S. salmonis development is characterized by eight identified stages separated by moulting. There are two stages of the newly hatched nauplius larvae. The second nauplius stage is followed by a single copepodid stage. This is the infectious stage, at which the louse is able to attach and initiate relationship with a potential host. Within acceptable temperature ranges, the infectious copepodid can survive in the marine environment up to 7 days without a host (Stucchi et al 2011). The nauplius and copepodid stages are non-feeding, planktonic organisms drifting passively on the upper water column mainly at the mercy of the wind and ocean currents, but also have a number of host-seeking behaviours. (Costello, 2006; Jones and Beamish, 2011, p. 5)

The transmission and dispersion of planktonic larvae and infectious chalimus is still a matter of ongoing research, but we know that wind patterns and tidal currents play a major role in the horizontal passive transport of planktonic sea lice. Data predicts an average dispersal distance of 12 km distance in low currents (~5 cm s^{-1}) and up to 70 km in higher currents (~20 cm s^{-1}) (Costello, 2006). The variability and complexity of local hydrographic conditions, especially in the fjords, makes predictive modelling of dispersal difficult.

L. salmonis is able to actively move vertically in the water column, further increasing the chance of host contact (Heuch et al., 1995). Heuch et al revealed that both the nauplius and copepod are positive phototactic, migrating towards the water surface during daylight and sinking during darkness. This pattern was more pronounced during the copepod stage. It should also be noted that this is the opposite to the light-induced migration pattern we see in wild salmonids. Descending salmonids meeting ascending lice during daylight hours and vice versa during dark, possibly increasing the chance of parasite-host interactions. (Heuch et al., 1995)

Host-seeking lice are in general most abundant towards the water surface, at a depth of between 0-4 meters ((Mordue (Luntz) and Birkett, 2009). In case of sudden changes in water currents or mechanical vibrations, such as with bypassing fish, the larvae were found to respond with a swimming-burst towards the source. When non-parasitic parasitic copepods (Acartia sp.) were exposed to the same stimulation, escape behaviour was observed (Heuch et al., 1995).

L. salmonis copepodids has also been found to respond with increased movement activity at exposure to host-derived chemical substances. In the presence of substances from non-salmonids, the increase in activity was eliminated. This chemoreceptive mechanism may help the parasite in confirming correct host after attachment (Bailey et al., 2006). Other cues involves the photoreceptive detection of light levels and reflective patterns of the salmon in the water (Browman et al., 2004). Knowledge of larval dispersion is essential in developing accurate models predicting local infection pressure, as explained further in chapter 5.

Upon contact and chemoreceptive confirmation of a susceptible host, the copepodid will use its antenna to penetrate the host epidermis. An adhesive secretion will harden and form an anchor point between the parasite and the fish skin. After tethering, the two chalimus phases follow. During the copepod and chalimus stages, the lice will stay tethered to the host with its frontal filament and feed on the fish mucus and skin locally. (Jones and Beamish, 2011)

During development into the next stage, the louse will lose its frontal filaments and enter what is called the ‘mobile phase.’ The mobile phase is comprised of two pre-adult stages and the final adult stage. While moulting during these stages, the louse will re-attach to the fish with chalimus-like frontal filaments (Costello, 2006). The mobile *L. salmonis* use suction generated by the cephalothorax and supporting morphology to maintain fixed to the fish while moving freely around feeding on the host mucus, skin and blood. The head and dorsal surfaces of the host are main predilection sites for the pre-adult and adult stages (Jones and Beamish, 2011)

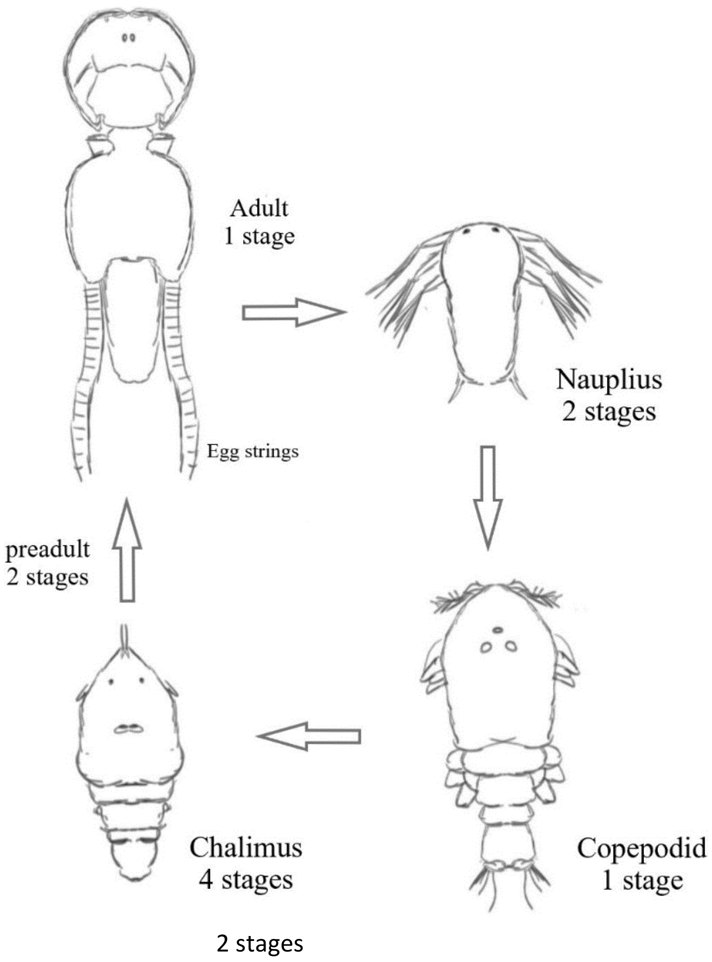

Figure 1. Life cycle of Lepeophtheirus salmonis, represented with 8 stages. (redrawn from Jones and Beamish 2011)

Hamre et al. 2013 argued that there are only two chalimus stages, opposed to the four previously suggested. The difference is significant regarding future research and the development of management strategies. It seems that most sources published after 2013 operate with two chalimus stages. (Hamre et al., 2013, p. 2; Ohtsuka et al., 2009).

Aquaculture impact on *L. salmonis*

Organisms are expected to adapt and respond to changes in their environment, and in this case, it is relevant to study the physiological alterations induced by the aquaculture industry on *Lepeophtheirus salmonis* in order to understand emerging challenges and prepare relevant strategies for monitoring and management.

Effect on reproduction

Compared to the lice originating from farms, the non-farmed lice are more challenged with finding a new host after hatching and dispersing. Because of the lack of delousing treatments, the life expectancy of the non-farm lice is likely longer than the farmed lice. A study was performed in 2017 comparing selected traits in lice from farmed locations with that of unfarmed locations (Mennerat et al., 2017). The study examined how the louse adapted to this shift in terms of development and reproductive features.

The parameters investigated were infection success, fecundity and adult survival rate. The studies revealed an increased fecundity in the farmed lice compared to the wild during the first reproductive event, but lower during the second and third. The lice from farmed areas had higher infestation intensity during early age, but also higher adult mortality. The results indicates how the farmed lice, in expense of adult survivability and late fecundity, invest in early reproduction in response to the shortened life expectancy (Mennerat et al., 2017).

Effects on drug resistance

When *L. salmonis* emerged as a major problem, anti-parasitic chemicals were introduced as a successful method of choice for sea lice management. Exposure eventually led to genetic resistance mechanisms in the lice, driven by the survival and reproduction of the less sensitive individuals (Aaen et al., 2015). It is important to diagnose the resistance problem as early as possible in order to initiate better management strategies to control its extension (Kaur et al., 2017). Later chapters elaborate how resistance is monitored and controlled in official programmes in Norway.

Resistance against specific pharmaceuticals have been reported short time after their respective introduction, and shifting towards new anti-parasitic chemicals and methods have been continuously required. There are major resources invested into investigating the specifics mechanisms and genetics responsible for development of resistance as an important step in establishing improved strategies for management and prevention.

Some mechanisms have already been identified, including the overexpression of metabolic enzymes inactivating emamectin benzoate (Aaen et al., 2015), mutations of the voltage-gated sodium channels in pyrethroid resistance (Carmona-Antoñanzas et al., 2019) and a single mutation of the acetylcholinesterase enzyme in organophosphate resistant lice (Kaur et al., 2017).

Effects on virulence

In a study from 2017, Ugelvik infected Atlantic salmon smolt with collected samples of *L. salmonis* from both unfarmed and farmed areas. He compared the skin lesions and the growth of the two groups of fish in order to evaluate the virulence of the lice. The study revealed that the skin lesions were more severe, and the relative weight of the host was reduced to a greater extent in the farmed lice. (Ugelvik et al., 2017)

The farmed lice have, as previously explained, shortened lifespan-expectancy due to treatment regimens and regular slaughtering of hosts. Ugelvik mentions that similar trends (increased virulence associated with shortened lifespan of agent or host) are suggested in other parasitic agents, such as the increased virulence of Marek's disease virus of poultry associated with vaccination and shorter host lifespan selection.(Atkins et al., 2013)

Pathogenicity

Direct effects

Direct mechanical effect from the feeding activity and attachment mechanisms of mobile phase lice is what causes the typical pathology associated with *L. salmonis* infestations. Usually only minor local inflammation and hyperplasia can be seen at the filamentous attachment sites when only pre-mobile larvae are involved. The degree of tissue response varies depending on host species, being more severe in the Coho salmon compared to that of the Atlantic salmon. As previously mentioned, greater tissue response is associated with higher louse mortality and decreased susceptibility. (Eva et al., 2014; Fast et al., 2002)

Common pathological lesions involve the skin of the body and fins, ranging from mild inflammation and erosions to sloughing and large open wounds. Lesions may be further complicated with secondary bacterial infections or fungal infections once the fish return to freshwater. Secondary osmoregulatory dysfunction and anaemia may also develop. (Jones and Beamish, 2011; Wagner et al., 2008). We rarely see such lesions on farmed fish due to strict regulations on lice numbers and treatment procedures.

Osmoregulatory disturbances

Barrier reduction between the sea water and the fish' internal milieu is associated with the severity of mechanical skin trauma caused by *L. salmonis*. (Ugelvik et al., 2017). No significant increase in plasma chloride (indicative of osmoregulatory disturbance) or plasma cortisol was evident before the lice developed into the mobile pre-adult stage (Wells et al., 2006). Mobile infestations are more likely to cause more severe skin lesions, and consequently cause osmotic disturbances and increased morbidity. Wagner et al found the abundance of lice causing osmoregulatory imbalance in the host to be between 0.5-2.1 lice g^{-1} (Wagner et al., 2003).

Wells et al performed a study on the lice-induced stress response in brown trout smolts in 2006 and he found that mobile lice stages were associated with prolonged increased levels of plasma cortisol in the affected fish (Wells et al., 2006). Earlier studies have linked chronic stress in fish to osmoregulatory disturbances and pathological gill changes (Wendelaar Bonga, 1997). This suggests that the physiological stress response induced by the presence of lice may, in itself, be a contributory factor of osmoregulatory dysfunction.

Impaired immune response

A study on 200 Rainbow trout revealed an impairment of macrophage host defence mechanisms after the sea lice became mobile. The impairment was observed to predispose the fish to infection by the microsporidian parasite, *Loma salmonae*. (Mustafa et al., 2000)

Another study recently confirmed the suspected correlation between positive sites or subsequent clinical outbreak of Infectious salmon anaemia (ISA) with the presence of salmon lice infestations. Exposure and infection of *L. salmonis* prior to exposure of ISA virus significantly increased the mortality and death rates compared to the control groups. They observed a down-regulation of anti-viral response genes in the infested fish prior to and following ISA infection. It was concluded that the manipulation of host immune system following the infestation of *L. salmonis* increased the host's susceptibility to ISA. ISA is an OIE-listed disease of major concern in Norwegian aquaculture (Barker et al., 2019).

Other Subclinical effects

Wagner et al performed a study in 2003 on the swimming ability and cardiac performance of Atlantic salmon infested by *L. salmonis*. The critical threshold for clinical infection had previously been estimated at 0.75 lice g^{-1}, but he demonstrated that even a sublethal infection at 0.1 lice g^{-1} impacted the overall fitness of the fish. An altering of cardiac performance and 19-22% decrease in swimming performance was seen during exercise compared to unaffected fish (Wagner et al., 2003). Swimming performance is of major importance in the reproductive fitness and survival of the wild fish, especially considering its migratory life history.

L. salmonis Impact on wild salmonid populations

L. salmonis from fish farms is recognized as a major threat towards wild anadromous salmonids on the Norwegian coast. As previously mentioned, studies have shown a clear correlation between increased salmon lice abundance on wild salmonids with farm proximity and the aquaculture industry's development. The effects on the individual fish is well-documented, but field-studies on wild salmonid population is difficult and somewhat lacking. (Halttunen et al., 2018; Jones and Beamish, 2011).

To grasp the impact of *L. salmonis* on the wild host populations, it is important to understand their natural migratory anadromous behaviour. Every year during spring and early summer, the Atlantic salmon smolt migrates from their native rivers towards ocean feeding grounds. When the salmonids pass through aquaculture-dense areas on their migratory path, they encounter large numbers of farm-derived infectious *L. salmonis* copepodids. The sea trout often remains in the coastal areas, usually within 80 kilometres from their home river, potentially increasing their exposure-time to the infectious larvae (Thorstad and Finstad, 2018). Field observations and studies have shown that lice-exposed sea trout migrate back towards the river outlets and estuaries earlier compared to control groups, at the cost of increased mortality and reduced growth rate (Whelan, 2010).

The fishes may already be subject to increased mortality due to the challenging physiological process of parr-smolt transformation or predation (Taranger et al., 2015), and exposure to *L. salmonis* may further contribute to increased mortality.

Not much is known about the details concerning the behaviour and environmental factors influencing wild sea trout and Atlantic salmon during the early sea phase, but a study performed by Skaala, involving treating, releasing and re-capturing individuals demonstrated that the survival of Brown trout smolt treated with anti-parasitic drug before release was nearly doubled in comparison with the control group. This is likely the first study documenting mortality in trout population induced by *L. salmonis* on an intensively farmed area. Similar results were achieved on a study on Atlantic salmon, where the return rate on treated fish compared was shown to be 1.8:1 compared to the control. This is indicative of *L. salmonis* outbreaks representing an important factor in regulating population levels of both the Atlantic salmon and the Sea trout. (Gargan et al., 2012; Skaala et al., 2014)

Population level impacts will only occur when above a certain threshold of intensity, and when affecting a significantly large portion of individuals. (Taranger et al., 2015)

Risk evaluation for wild salmonids in Norway is based on a system proposed by Taranger et al, assuming fish weight and lice abundance corresponds with an estimated mortality rate or premature return to estuary in post-smolt individuals, or mortality and compromised reproduction in larger salmonids. The assumption must be made that the individuals caught are representative for the population in the specific area. (Taranger et al., 2015)

	<150g post-smolt weight	*>150g salmonids*
100% mortality	>0.3 lice g^{-1}	>0.15 lice g^{-1}
50% mortality	0.2-0.3 lice g^{-1}	0.05-0.10 lice g^{-1}
20% mortality	0.1-0.2 lice g^{-1}	0.01-0.05 lice g^{-1}
0% mortality	<0.1 lice g^{-1}	<0.01 lice g^{-1}

Figure 2 Risk assessment of fish linked to abundance and fish weight. Data from Taranger et al 2015

This risk assessment is performed constantly as a part of a national monitoring program of sea lice impact on wild salmonids, evaluating wild fish from sentinel cages and trawls. The data is put into further context with the larvae dispersion model described in the next xhapter (Nilsen et al., 2019).

An annual report designates a risk-evaluation on each of the thirteen geographically determined production zones, defined as low (below 10%), moderate (10-30%) or high (>30%) based on Taranger et al' assessment. The most recent report from 2019 showed low risk profile in eight out of the thirteen production zones, moderate risk in four zones and high risk in only one zone. The most severe infectious pressure was observed along the western counties of Norway, specifically in Nord-Hordaland and Sogn. The least affected areas were the northern- and southernmost production zones, which also are the zones with the least farm density. (Nilsen et al., 2019).

Sea lice monitoring programs

Farm monitoring

The development of a national monitoring program started in 1997, under the National Action Plan report of 1996. The goal was to reduce the impact of *L. salmonis* on both wild and farmed fish, and for it to be used as a planning- and coordination tool for the industry. The regulations and methods have since changed in accordance with our increasing knowledge of *L. salmonis* and during development of the epidemiological status. (Jones and Beamish, 2011, p.159-162)

The Norwegian national Institute of Marine Research initiated a project in 2012, involving the weekly collection of data from every farm location within the country. All farms became obliged to manually count and report lice-abundance from at least 10 fishes to the authorities every week in sea temperature above 10ºC, and every other week if between 4 and 10ºC. The number of sexually mature female lice is used to estimate the number of infectious larvae produced from each farm. (Guarracino et al., 2018)

The data gathered is being used in data modelling and is published on a website open to the public, allowing everyone to view and evaluate information on the level of individual farm locations. Available information includes the at-site abundance of lice (categorized by sex and stage) and the method and frequency of delousing treatments performed. ("Lusedata," n.d.).

Wild fish population monitoring

In order to support a sustainable growth of the aquaculture industry, a new management system was established in Norway in 2014 (Guarracino et al., 2018) The “traffic light” system was designed to predict the increasing risk of critical influence by *L. salmonis* on the wild fish population and thereby determine whether the salmon production capacity in each zone can be increased (green light), remain unchanged (yellow light) or be decreased (red light). Thirteen production zones were established based on larvae distribution models, predicting that 95% of larvae produced would stay within the specific zone (Guarracino et al., 2018). Observational and numerical model data gathered by previously mentioned monitoring and surveillance programs is evaluated by expert groups, which recommends a “traffic light”-status on the specific production zone. The decision is later formally determined by the Ministry of Commerce and Fisheries.

Creating models that can accurately describe and predict the extension of *L. salmonis* distribution is an essential step in developing management strategies and preventive measures against the parasite. In 2018, the institute updated their dispersion model of salmon lice copepodids along the Norwegian coast. The system uses a system of individual particle tracking, implementing the combined knowledge of *L. salmonis*’ behaviour, growth and mortality with real-time information on variable factors such as wind and currents, temperature, salinity and freshwater runoff (Myksvoll et al., 2018)

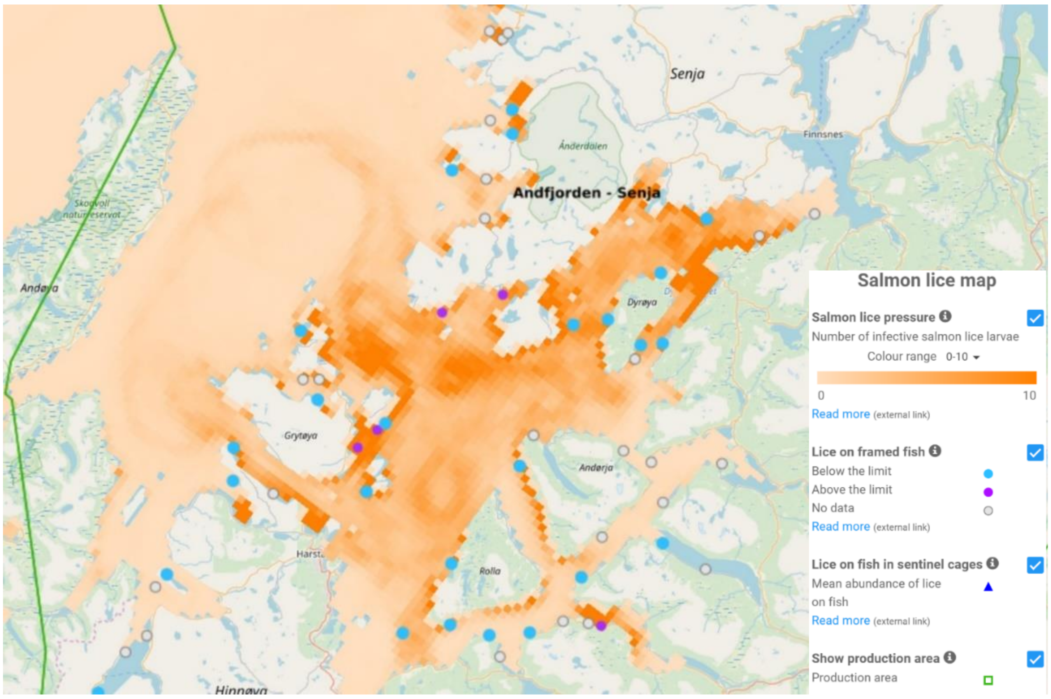

Figure 3 Snapshot from the National marine Research institute website, showing the infectious pressure of L. salmonis by the island of Senja during week 42, 2019 (https://www.hi.no/forskning/marine-data-forskningsdata/lakseluskart/html/lakseluskart.html#)

In addition to using models and theoretical data, the institute evaluates the in-field status by performing lice counts and health evaluations of wild salmonids. Sentinel cages stocked with salmon smolts are placed in the fjord systems for 3 weeks before the abundance of lice is counted and evaluated. Wild fish are also being caught using special trawls to evaluate the infection pressure in specific areas. There is a strong correspondence between field reports and the theoretical dispersion model, making it a very useful tool in infestation pressure mapping and management. (Myksvoll et al., 2018)

Drug resistance monitoring

In order to get an overview of the national drug resistance status, the Marine research institute launched a monitoring program in 2013. This program is still active and involves both the passive monitoring of prescription data, and actively performing molecular and toxicological studies of lice from representative farms along the coast. An annual report is regularly published on the status of resistance against the most important chemotherapeutants currently in use (Grøntvedt et al., 2016).

Based on reports from the surveillance program, a peak in both infection pressure and drugs prescribed against *L. salmonis* was recorded during 2012-2014, causing a significant increase of drug resistance in the following years. Since 2015 there has been a major shift from the traditional medicinal treatments towards other options like continuous delousing with cleaner fishes and mechanical delousing procedures. (Tarpai et al., 2019). During the period 2014-2018 the total number delousing prescriptions was reduced by 86%.

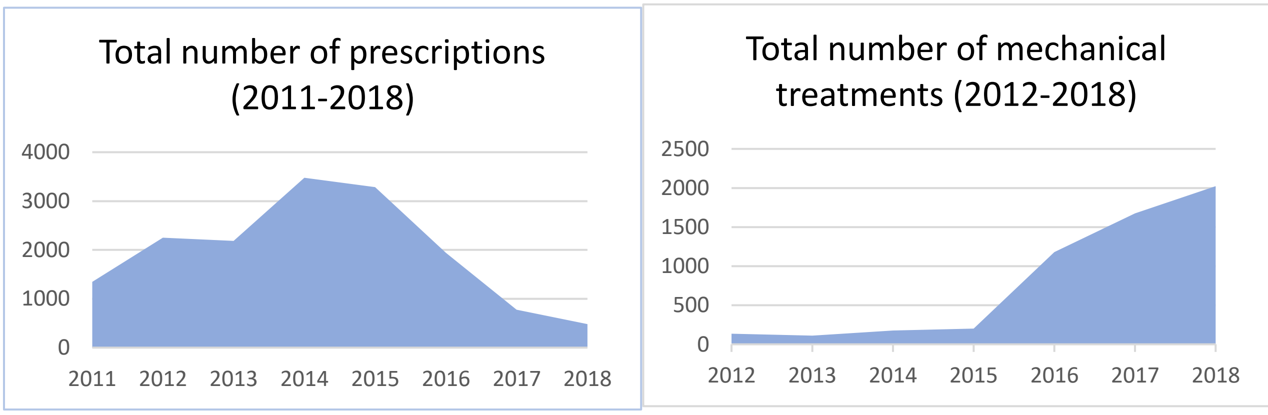

Figure 4 Side-by-side comparison of number of medicinal and mechanical treatments performed during 2011-2018

A general tendency of reduction in drug resistance was observed in the 2017 report, and the trend has been observed to continue in 2018. This is most likely a result from the reduced prescription frequency and increased demand for mechanical alternatives. Even so, resistance towards deltamethrin, azamethiphos and emamectin is still widespread. The lice show less sensitivity against hydrogen peroxide in certain zones, but in general hydrogen peroxide remains effective.(Grøntvedt et al., 2016; Tarpai et al., 2019)

Treatment and management

General considerations

Several factors must be considered when determining the optimal system of treatment against *L. salmonis*. Boxshall and Defaye (1993) mentions eight important factors; (1) lice removing efficacy, (2) stress caused to the fish, (3) financial costs, (4) staff hazard, (5) environmental effect, (6) availability, (7) marketing implications and (8) ease of application (Boxshall and Defaye, 1993).

Efficacy is indicative of not only the number of lice removed, but also what life stages are affected. If the method of choice is primarily effective against mobile stages, another treatment may be necessary a few weeks later after the chalimus larvae have developed into new pre-adult and adult lice, but in order to prevent resistance, the same treatment methods should not be repeated for a longer period in one area.
Withdrawal periods must be respected and timed according to the planned slaughter date. Treatment induced mortality should be avoided and the method chosen should cause minimal stress to the fishes, especially in stocks with poor health status and lowered stress tolerance. Temperature must be taken into account as trauma from crowding or mechanical treatments will heal slower in reduced water temperatures, making the fish increasingly susceptible to secondary infections (Overton et al., 2018a).

Medicinal treatments

Chemotherapeutic agents have traditionally been the method of choice in the management of sea lice, with the goal of decreasing the presence of gravid female lice and prevent the establishment of internal infestation cycles. The two main methods of application for delousing treatments include topical bath treatment and in-feed additives. Bath treatments involve exposing the lice directly to the active substance either by distributing the drug into a tarpaulin-enclosed cage, or by pumping the fish onboard a well-boat. Until the appearance of resistant lice, bath treatment has been an effective measure in lice management. It is, however, labour-intensive, expensive and time consuming. Oral application is more practical in use and less stressful to the fish compared to topical delousing processes.(Jones and Beamish, 2011; Overton et al., 2018a)

Topical treatment

Pyrethroids

Pyrethroids are a group of synthetic pesticide analogues, derived from the plant *chrysanthemum cinerariaefolium*. They have been deemed suitable for aquaculture due to their toxic effect in crustaceans, easily degradable structure and high safety in mammals (Overton et al., 2018b). It is believed that pyrethroids function by binding sodium channels in the organism, leading to paralysis and ultimately death (Bakke et al., 2018). Deltamethrin and cypermethrin are the most widely used pyrethroids in Norwegian aquaculture, being effective against preadult and adult stages of *L. salmonis*, but less so against chalimus lice stages (Whyte et al., 2014).

Organophosphates

Azamethiphos is the mainly used organophosphate, effective against the mobile pre-adult and adult *L. salmonis*. Organophosphates functions by inhibiting acetylcholinesterase activity, causing effective paralysis within a few hours ("Preparatomtale (SPC) | Salmosan Vet® - Sea Lice Treatment," n.d.). The toxicity of organophosphates is believed to increase with treatment water temperature for both the lice and salmon. A declining trend in usage is also seen on organophosphates with only 160kg Azamethiphos in total prescribed in 2018, a 96.5% decrease from the 2014 peak (Horsberg and Bangen, 2019).

Hydrogen peroxide

Hydrogen peroxide was the preferred topical delousing substance until it was replaced by pyrethroids and organophosphates. Its usage reappeared in Norway when widespread resistance to other drugs became an emerging issue in 2009. Following the 2015 resistance spike, the consumption of hydrogen peroxide plummeted along with all other chemical methods. The specific mechanism of action for hydrogen peroxide is not known, but oxygen bubbles in the haemolymph seem to cause mechanical paralysis. Hydrogen peroxide has long been considered the most environmentally friendly agent because of its rapid disassociation and lack of bioaccumulation, but recent studies elaborated in the next chapter have demonstrated the presence of significant risk (Fang et al., 2018; Overton et al., 2018c; Tarpai et al., 2019).

In feed additives

Administration of in-feed additives is less complicated than bath treatments and can be used also in challenging weather conditions, but reduced appetite in the fish will negatively affect the treatment efficiency. Emamectin benzoate is the most frequently used in-feed additive, followed by the chitin synthase inhibiting drugs diflubenzuron and teflubenzuron. After consumption of the medicine-coated pellets, the active substance is distributed in the tissues of the fish, including the skin. All chalimus, pre-adult and adult stages of *L. salmonis* are affected. In case of emamectin benzoate, the effect lasts for up to 10 weeks post-treatment, making it particularly useful for smolt treatment prior to seawater transfer. (Jones and Beamish, 2011).

Figure 5 Observational photo of a hydrogen peroxide bath treatment process (September, 2019, Senja). Photo from personal archive.

Medicinal threat to the environment

Potential negative environmental effects must always be taken into consideration in the management of *L. salmonis*, especially upon the use of medicinal treatments as they may affect non-target organisms such as coastal shrimp and other crustaceans. The Norwegian Seafood Research Fund (FHF) is a state-owned company dedicated to the further development of Norwegian aquaculture, including the provision of research and knowledge related to its environmental impact.

A study was recently performed by Norwegian Seafood Research Fund examining the effect of the three most common bath agents previously mention on egg-carrying shrimps, *Pandalus borealis*. The results demonstrated susceptibility towards all three chemicals, but their effective concentrations differed significantly. Deltamethrin was proven to be the most toxic substance, causing close to 100% lethality after two-hour exposure of 330 times recommended treatment dilution. The synergistic use of H_2O_2 and azamethiphos (500 times diluted treatment concentration) induced 50% mortality in the shrimps after one week, but no negative effects could be observed on the surviving shrimps. No sub-lethal or reproductive deficiencies were observed on surviving individuals after exposure to any of the chemicals (frantzen et al., 2019).

As previously mentioned, hydrogen peroxide has long been regarded to be the most environmentally friendly bath treatment alternative available. It was, however, revealed to have a longer half-life duration in the sea environment than previously expected in a study from 2016. Another study from 2018 examined the acute toxic effect of hydrogen peroxide in representative polychaete worms of species *Capitella* and *Ophryotrocha*. High mortality and irreversible damage were observed in both species after 1-hour exposure, and the surviving individuals after exposure did not survive the recovery period. The hydrogen peroxide concentrations evaluated were considered realistic and ecologically relevant in a treatment point of view. (Fang et al., 2018).

The issue of widespread drug resistance has led some actors the industry to change treatment concentrations beyond recommended values, or to use combinations of different drugs. There is a deficiency of off-label documentation in these drugs, significantly increasing the risk of fish mortality and negative environmental effects. Studies like these are performed in order to draw a more accurate picture of aquaculture sustainability and provide a basis for future risk-reducing regulations and recommendations. They may also act as a tool in reducing the level of conflicting interests between different aquaculture actors, such as the coastal fishing industry.

Non-medicinal delousing methods

Rinsing fish

The problems associated with increased resistance have led to the development of several alternative methods of treatment and prevention of salmon lice. Cleaner fish are currently extensively used as a measure of continuous lice removal, both caught wild and farmed. Different species of wrasse and lumpfish are used, with *Labrus bergylta* and *Cyclopterus lumpus* being the most common. The wrasse species are temperature sensitive, and unfit for use during colder months whilst the lumpfish is effective all year around and therefore preferred (Powell et al., 2018).

The lice-consuming effectivity is highly variable between individual farms. The lumpfish are opportunistic feeders, consuming salmon pellets and other organisms found in the pens as well as lice. The lice-rinsing behaviour abilities in lumpfish probably have components in both genetics and learning, indicating a potential of breeding programmes for improved effectivity in the future (Powell et al., 2018).

Introduction of a new fish species in the caged pens brings new challenges concerning sustainability, welfare and disease management. The species are susceptible to a wide array of diseases and have other environmental and nutritional requirements than that of the farmed fish. The cleaner fish industry have experienced an exponential growth, with approximately thirty million lumpfish and one million Ballan wrasse commercially farmed and delivered to farms in Norway during 2018(“Use of Cleanerfish 1998-2018,” 2019), as opposed to only a few thousands in 2010. The lumpfish is classified as Near Threatened on the Red Data list, with an estimated 25-35% decline in abundance over the last 20 years (Powell et al., 2018)

Although cleaner fish are already widely used in Norwegian aquaculture, future studies and attention is required for optimizing its function and production without compromising wild stock populations or fish welfare.

Mechanical methods

There are currently three main types of mechanical delousing processes available in Norway. Each of the systems are designed and licensed by different companies. The techniques developed by Flatesund engineering AS (FLS®), Skamik® and Hydrolicer® all involve the crowding and pumping of fish onboard designated delousing vessels. FLS-vessels are equipped with pressure washers that flush the lice away from the fish as they pass through a system of pipes. Water from the flushing process is filtered and the lice is collected and disposed of to prevent re-infestation. Skamik® uses the same principle as FLS®, but includes an additional system for brushing. Hydrolicer® uses inverse water turbulence to remove the lice by 'vacuuming' the lice from the fish' skin. (Overton et al., 2018b)

Table 1 Efficacy of FLS and hydrolicer delousing systems. There are no independent reports on Skamik efficacy.

	Stationary stages	Mobile stages
FLS ®	76-91%	81-100%
Hydrolicer ®	73-83%	78-95%

(Erikson et al., 2018; Overton et al., 2018b)

Thermal delousing

Thermal delousing was launched as a fish welfare- and environmentally friendly delousing alternative in 2015 and has since then become the most frequently used non-medicinal method in Norway. *L. salmonis* is sensitive to change in temperature, causing inactivation and detachment after short exposure, whilst the salmon is more resilient to temperature changes. Like the previously mentioned mechanical processes, the fish are crowded before they are pumped through a treatment chamber. The temperature of the treatment chamber is dependent on the sea temperature of origin, but normally varies between 28 and 34ºC and the duration is usually set to 20-30 seconds (Gismervik et al., 2019; Overton et al., 2018a). The water from the treatment is removed and the detached lice are filtered out.

Several studies suggest the treatment method is not as fish friendly as previously believed, causing major protests and national media attention. The method was labelled a torture chamber by animal protection services (Berge, 2019). The Norwegian food safety Authority recently issued a plan for phasing out thermal delousing above 28ºC within the next two years (“Termisk avlusing: Fiskevelferd, forskning og avklaring fra Mattilsynet | Mattilsynet,” n.d.).

A recent study from 2019 examined the behavioural response after direct transfer into high temperatures ranging from 0-38ºC. The threshold at which strong behavioural responses reflecting nociception was found to be between 28-30ºC, well within temperatures used for commercial thermal delousing. This behavioural response may lead to mechanical damage and possibly explain the relatively high mortality associated with thermal delousing. (Nilsson et al., 2019). Temperatures above 34ºC was observed to cause macroscopic visible bleedings of the gills, and histologically visible congestions, epithelial damage, necrosis and oedema. Acute tissue injuries to eyes, brain and possibly nasal cavity was also reported. (Gismervik et al., 2019)

Freshwater bath treatment

Freshwater treatment has great potential as delousing method and is currently being used and tested in Norwegian salmon aquaculture, contributing to 5% of all 2018 non-medicinal delousing treatments. The technique involves pumping the fish aboard well-boats where they are exposed to freshwater baths for 5-8 hours, causing most attached sea lice to detach and then filtered from the water. (Groner et al., 2019)

There is, however, a major drawback to this method regarding resistance. The appearance of freshwater tolerant sea lice, as seen in chemotherapeutants, would be potentially catastrophic for wild salmonid populations. The wild salmonids ability to remove the lice naturally in freshwater streams may decrease, and the infectious pressure could increase due to larger areas of the fjord being suitable for supporting larval stages. (Groner et al., 2019)

The Norwegian food safety authorities have issued treatment recommendations for precautionary use until further research has proven the method to be safe. (“Lakselusen kan øke sin toleranse for ferskvann | Mattilsynet,” n.d.).

Optical delousing

A patented device for optical delousing is currently being tested in 170 Norwegian salmon pens. The system utilizes a movable device equipped with cameras and artificial intelligence to continuously identify and remove individual lice on the surface of the fish host. A laser pulse of a specific intensity and duration is targeted directly on the parasite without harming the fish. The system can also be used for monitoring and registering lice number on live fish without removing it from the water. There are no studies presently available on the effectivity of the system. (Beck, 2015; Witzøe, 2019)

A report by Nofima (Institute of research) states, based on farmer experience, that the current device is not sufficiently effective during the most intense infestation periods and must be supplemented by other treatment options. They have observed good results when combining optical delousing with the presence of cleaner fish. The major benefit of this method lies in its ability to remove lice without any handling interventions of the fish or the use of chemicals or pharmaceuticals. (Holan et al., n.d.).

Functional feeds against salmon louse

All the three major fish food companies in Norway offer non-medicinal feed dedicated to reducing the infestation levels of *L. salmonis*. Due to market competition, the companies are very secretive about the components and specific mechanisms of their functional feed and most research performed is never published. Probable mechanisms may involve immune-stimulative effects, improvement of mucous and barrier functions and the camouflaging of specific chemical signals or pesticidal effects. The effect of the different feeds is not well documented, but the producers themselves report 20-30% effectiveness during field trials. (Holan, 2017)

Preventative measures

Physical barriers

The strategy of preventing infestation can be done by physically separating the fish from the infectious copepodids. It is possible to establish a barrier between the host and parasite, but it should not compromise the fish health and welfare. Such new technologies of rearing are currently considered more advanced and expensive than open net cages, but may, nonetheless, become a necessity in the future. Louse skirts, snorkel- and submergible cages are currently the three leading methods of effective separation.

The use of cage-surrounding semi-permeable skirt is the only commonly used and well-studied measure, acting as an effective physical barrier around the otherwise open cage. An average infestation reduction of 28% and 49% with six- and ten-meters deep skirts respectively has been reported.(Holan, 2017) The barrier may adversely affect the oxygen level in the cage by altering water flow-through so that monitoring and oxygenation methods may be required, especially during periods of higher water temperatures. (Grøntvedt et al., 2018)

Snorkel cages and submergible cages works by the principle of keeping the fish biomass situated lower in the water column than the infectious copepodids, thus preventing infestation. The snorkel cage has a closed cylindrical path to the surface for allowing fish to maintain swim-bladder equilibrium. Submergible cages actively let the fish up to the surface at specified time intervals. Submerging the fish may also solve other problems such as exposure to jellyfish and toxic algal bloom (Glaropoulos et al., 2019). Both these methods of keeping are still in a developmental phase and not yet commercially used. There are no present studies documenting the effect of the submergible cages, but snorkel cages show a consistent 75% average reduction of newly attached lice in compared to the current standard (Geitung et al., 2019).

Synchronized delousing

One of the main reasons for establishing the previously mentioned production zones was to enable the coordination of louse management within the defined areas. Not much studies had been performed on the effect of coordination when the zones were first established in 2010. Two zones (Hardanger and Vikna) were chosen to perform obligatory coordinated fallowing from 2012 to 2016, and data was collected for future evaluation. The coordination of management has not been regulated in any other sites than Hardanger and Vikna since, and is not frequently performed in other production zones. (Jones and Beamish, 2011, p. 174)

In 2018 the data collected from the coordination zones was analysed and evaluated by Mario Guarracino et Al. The evaluation raised serious doubt about the effectiveness of synchronized fallowing. The synchronized increase of fish biomass in the oceans at the beginning of grow-out period was associated with an explosive growth of lice population. The fish may have been infested soon after stocking as it has been shown that salmon lice larvae may drift up to 100 km distance in the Hardanger zone, and the farms were not sufficiently sheltered. There were no data-trends suggesting any reduction in infestation pressure in neither of the production zones (Guarracino et al., 2018)

Future management options

If the aquaculture industry is unable to establish sustainable production on the coastal areas, we must find alternative methods of rearing fish in order to develop the production further. Moving the entirety or parts of aquaculture production to closed containment farms on land or further out in the ocean may be a potential future solution. The first onshore location in Norway started production in May 2019, and currently the operation is going well. The fish will be kept onshore until it reaches 1 kg bodyweight before transported offshore where it stays until slaughter. At 1kg the fish is healthier, more robust and more resistant to salmon lice infestation when delivered to the offshore cage. Rearing fish at slaughter weight demands large amount of space, representing a big problem on land. Full onshore production methods are still in a developing phase, but might become reality in the future. (Lilleholt kraugerud, 2019; Riise, 2019)

Research is currently being conducted in the development of a salmon lice vaccine. The trials are still at an early stage, but lab-scale tests have shown good potential by affecting abundance of female lice and its fecundity. Effects are also seen on the second-generation lice. An effective vaccine would be a cost-effective method of controlling infestation without the use of chemicals or any known environmental effects. (Swain et al., 2018)

Figure 6 Adult female L. salmonis carrying egg-strings. Picture from personal archive

Summary

L. salmonis is a notorious parasite known to affect the two major cultured fish species in Norwegian aquaculture and wild stock populations. The first chapter of the thesis explains the significance of commercial aquaculture in Norway and the importance of establishing a sustainable industry. The thesis describes the most important aspects concerning the biology and ecology of *L. salmonis* in context with its host and their shared environment. In order to understand the population dynamics and models of *L. salmonis* distribution, an overview of the dispersal and host-finding behaviour in the infectious larvae has been emphasized.
It is important to keep studying and continuously stay updated on aspects of lice biology, especially regarding the species' highly adaptable nature and the rapid development of the aquaculture industry.

Official monitoring programs *on L. salmonis* have been presented, describing the observed trends and present status on situations such as wild stock infestation levels, resistance status and the development in management and methods of treatment. The industry has yet to find a treatment strategy that is both fish welfare- and environmentally friendly, but emerging technologies such as the mentioned Stingray® laser system and development of vaccines may be part of the solutions in the years to come. The aim of management is not to eliminate the lice completely, as this is considered unfeasible, but rather to reduce the infectious pressure within sustainable levels.

In the past years, attention has been directed towards re-evaluating the concept of salmonid aquaculture in Norway. Environmental organizations and green political parties support the concept of closed-containment cages or onshore production units. Other major challenges with open net cages include organic pollution, escapees threatening the genetic integrity of wild stocks and the extensive use of area.

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