Master's thesis



Assessment of sea lice infection rates on wild populations of salmonids in Arnarfjörður, Iceland

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Declaration

I hereby confirm that I am the sole author of this thesis and it is a product of my own academic research.

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Abstract

Sea lice have had impacts of varying severity on both wild and farmed salmonids in the past and although research has focused on this particular parasite, problems are still present. Lepeophtheirus salmonis Krøyer is of special concern, as negative impacts on the host fish have been proven, which can threaten wild fish populations. While countries like Norway and Scotland were only able to react to the problems induced by sea lice epizootics, Iceland is in the position to take pre-emptive measures. The present study was a first step into this direction, as it assessed the infection rates on wild salmonids in Arnarfjörður, North-West Iceland. During the month of July and August fish were sampled by using gill nets at three different sites. Lice were counted, their life cycle stages determined and the results were compared to previous studies from other countries. This comparison showed that both prevalence and intensities for the sampled fish are similar to those values from fjords without salmon farms. An impact on infection rates from the existing farms in Arnarfjörður was not found, most lice seemed to mature in August and it was suggested that their offspring should be able to complete a full life cycle in the same year. Whether these results are valid for other parts of Iceland, has to be shown by future research and a more specific analysis, for example the use of hydrographic models or infection thresholds is recommended, especially if the salmonid aquaculture in Iceland continues to grow.

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1 Introduction

1.1 Wild salmonids around the world

Salmonids is the name of a specific group of fish that share similar traits. Amongst others this group includes Atlantic salmon (Salmo salar), sea trout (Salmo trutta) and Arctic char (Salvelinus alpinus) (Keeley & Grant, 2001). All of these species can be found amongst the waters of the northern hemisphere and have been recorded in various countries ranging from Portugal in the South to Iceland and Greenland in the North (Parrish, Behnke, Gephard, McCormick, & Reeves, 1998). Historically, the trout was only native to the eastern side of the Atlantic Ocean but has been introduced to the western parts by humans (Elliott, 1994). Opposite to that, Atlantic salmon and Arctic charr have been exploiting the whole range of the North Atlantic, Baltic and other areas (Hansen & Quinn, 1998) and their migration patterns are extensive. A population of one of these salmonids, as it is the same for any other animal, is referred to as a wild or natural population if it sustains itself and reproduces without any human influence. The three named salmonid species hold a high economic value in numerous countries, for example Norway, Scotland and Iceland. They can be observed and consequently caught in fresh-, brackish- and saltwater due to their anadromous life cycle (Klemetsen et al., 2003; Rikardsen, Amundsen, Bjørn, & Johansen, 2000). Their migrations lead them through all of those three habitats (Scott & Crossman, 1973), in which they remain for various amounts of time which will be further explained later on. As can be observed for other fish species, wild salmonid stocks have been decreasing in many parts (Reviewed in Mills, 2003). Wild populations have even been found to be extinct in countries like Germany and the Netherlands. In other areas like the US and Canada the population numbers are on a rapid decline (Good, Waples, & Adams, 2005). Healthy salmon populations seem to only exist in a few countries, namely being Norway, Ireland, Scotland and Iceland. This is only a valid statement for salmon, as trout populations in, for example, Scotland had experienced a dramatic decline in the past (Bricknell, Dalesman, O'Shea, Pert, & Mordue Luntz, 2006). Also, even these countries have been experiencing declines of populations in certain areas which has been related

to increasing fish farming activities (Costello, 2009a). Due to this fact fish farming and its possible influences on wild populations will be considered in this thesis as well.

1.2 Icelandic use of wild salmonids

All of the three named salmonids are native to Iceland making them three out of a total of five native species (Guðbergsson, 2014). Catching salmon in an open ocean fishery is not allowed in Iceland since 1932 and while sea ranching was in certain areas still allowed it is also banned now since 1997 (Guðbergsson, 2014). Bycatch of salmon in other ocean fisheries is negligible with an amount lower than 16 tonnes in 2005 (Guðbergsson, 2014). Open ocean fishery for trout and charr is not reported. Due to Iceland's geomorphology it has a high number of rivers that are directly connected to the ocean and that are suitable to host salmonids during the freshwater phase of their life cycle (Guðbergsson, 2008). In addition to that, there are also records of nonanadromous populations which use these habitats all year round. However they are not important for this thesis as they do not get into contact with sea lice. Fishing for salmonids in Iceland is restricted to freshwater and there it is mainly done by rodfishing. Net-fishing is generally forbidden and exceptions are only made for some highly turbid glacial rivers where usage of gill nets is allowed (Guðbergsson, 2014). There is a strict regulation regime in place which is controlled by the Directorate of Freshwater Fisheries. Fishing rights in Icelandic rivers are connected to land ownership adjacent to the river (Isaksson, 1979). By law all land owners, mostly farmers, that gain fishing rights in one river must form a fishery association. This association is then responsible for monitoring the fish stocks and keeping the fishing activities inside the frame that is given by the Directorate of Freshwater Fisheries (Guðbergsson, 2014). The length of the fishing season is also restricted and differs for salmon and trout. The former can be fished for a maximum of 105 days from the 20th of May to the 30th of September, while the season for the latter is from the 1st of April to the 10th of October with a possible 10 day extension that needs a separate allowance (Guðbergsson, 2014). Per day fishing can only be carried out for 12 hours and needs to be closed for at least 84 hours a week (Guðbergsson, 2014). How many rods are allowed per river is also

regulated by the Directorate but it does not matter if fishing is carried out by the landowners themselves or if fishing rights are sold to other people like tourists. This specific number of rods has been stable for rivers all over the country since the 1970's. In connection to that, the number of fish that are caught annually has been somewhat stable. Salmon catches depend on fluctuations between years due to changes in size of the salmon run. On average the amount of salmon caught and processed has been stable, with an increase of catch and release in the recent years. There is no evidence for a long-term decline in Icelandic salmon stocks, just the fluctuations which seem to reflect cyclical changes in the environment and are common for rivers in northern Iceland. (Scarnecchia, Ísaksson, & White, 1989) (Figure 1). Catch of trout has also remained stable for the first decade of the new century, approximately 40.000 fish per year, with a small decline in the following four years (Guðbergsson, 2014) (Figure 2).

As already mentioned it is allowed for landowners to rent out their fishing rights to other people. In a lot of Icelandic rivers this is a common practice and tourists are the main buyers for these rights. For the year 2003, the recreational angling industry already supported over 1000 jobs directly and had direct economic impacts of approximately 2 billion ISK (Agnarsson, 2005). During this one year, around 5000 to 7000 tourists came to Iceland just to do recreational salmon and trout fishing with rights they had rented from associations (Agnarsson, 2005). Looking at the tourist sector in Iceland, and the steadily increasing numbers in both visitors per year and money that is spent in Iceland by tourists each year, it is to assume that these numbers are even higher today. This makes the recreational angling industry an important part of the tourist sector and as such it has an importance for the Icelandic economy in general as it has been reported in other places (Butler, Radford, Riddington, & Laughton, 2009; Harris & Milner, 2006). An effect that especially has to be considered is that this sector brings money into more rural areas and unlike others not only to the capital region or main cities like Akureyri and Isafjordur (Toivonen, 1997). This is due to the fact that the expenditure for the angling license only compiles about 40 percent of the total expenditure (Agnarsson, Radford, & Riddington, 2008), with the rest going towards various other areas like grocery or equipment shopping. Any activities that can potentially have a negative influence on this sector are thus not wanted in Iceland and have to be observed closely to minimize or prevent their effects. One of these activities is fish farming, which will be referred to as aquaculture throughout this article. The negative effects that this activity can have on wild salmonid populations are various and one that has been the focus of research and concern is the increased production and release of the parasitic sea lice.

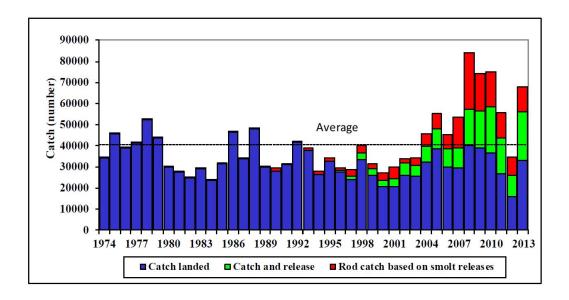


Figure 1: Salmon catch in rod and line fishery in Iceland 1974 - 2013. Catch landed (blue bars), catch and release (green bars) and catch in rivers with salmon fishery based mainly on smolt releases (red bars). (Guðbergsson, 2014)

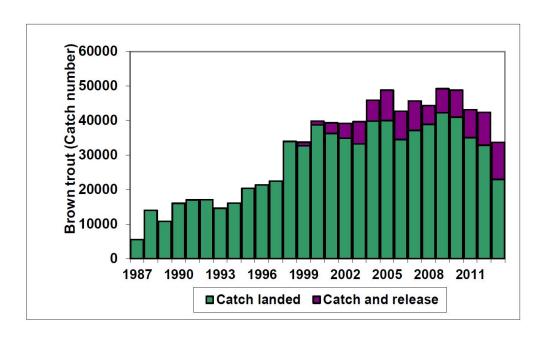


Figure 2: Catch landed and caught and released brown trout in the rod fishery in Iceland 1987-2013. (Guðbergsson, 2014)

1.3 Aquaculture

Aquaculture as a mean to provide seafood has been on the rise ever since wild fish stocks have been overexploited and do not yield enough or nothing at all. It is carried out in various forms, with salt- or freshwater, land- or sea-based and intensive or extensive. One species that has been used in many different countries is salmon. The worldwide production of salmon and especially Atlantic salmon grew from only 299 000 tonnes in 1990 to 1.9 million tonnes in 2010 (FAO, 2012). This equals an annual growth rate of more than 9.5 percent. In the North Atlantic region many countries have been using Atlantic salmon and one example that can be used for showing the growth of this business is Norway. The amount of salmon that is produced in aquaculture in Norway has been growing since 2000 (Norwegian Directorate of Fisheries, 2014a). Just as in other countries like Scotland, Ireland and Canada the amount of salmon that is present in aquaculture cages exceeds the respective wild populations by orders of magnitude (Butler, 2002; Heuch & Mo, 2001; Krkošek, 2010a). In Norway, the production is shifting towards bigger companies, a process that has also been observed in related sectors like agriculture. For the year 2010, the production of over 60 percent

of all salmon aquaculture had been done by only 10 companies (Norwegian Directorate of Fisheries, 2014b).

The Icelandic aquaculture sector is not as big as it is, for example, in Norway or Scotland but aquaculture has been present for many years as well. All three salmonids species that have been named already are present in aquaculture in Iceland. It is however, the case that charr is produced in land-based aquaculture where it does not come into contact with wild populations. This was also the case for sea trout but there have been recent changes which led to sea trout being only produced in ocean farms in the year 2012. Production numbers were 200 tonnes for 2011 and 446 tonnes for 2012 (OECD, 2013). The two main species in ocean pen aquaculture are cod and salmon. The latter had been farmed as the main species until 2006. In 2006, nearly 7000 tonnes of salmon was produced in aquaculture while the number for produced cod was only at 1412 tonnes (Table 1) (Figure 3). While the amount of farmed cod remained stable from that point on until at least 2009, the amount of farmed salmon decreased sharply to only 1158 tonnes in 2007 and 500 tonnes in 2009 (FAO, 2010) (Figure 3). In 2008, there were 12 registered sea farms in Iceland of which only one was using salmon (Paisley et al., 2010). Similar to sea trout the development in the recent years is also towards an increased amount of farmed salmon. Production had grown again to a number of over 3000 tonnes in 2012 and around 4000 tonnes were forecasted for 2013 (see **Figure 3**). This trend is still up to date which brings up the question of possible sea lice induced problems as they have been observed in other countries with salmon aquaculture and it is the main aim of this study to evaluate the current situation regarding the wild salmonid populations.

Conducting this type of research in Iceland has to the best of my knowledge not been done before and thus no reports of infection levels on wild populations exist. Sampling for sea lice is done however, in existing salmon farms in Arnarfjordur. As these farms are fairly new and have not been operating for a long time, these counts are from the recent past. Results of lice counts were accessible for the farm operated by Fjardarlax once in August and once in September while Arnarlax provided results for lice counts

on their fish once every month from July to October (**Table 2 & 3**). This data will be further discussed later on in this work. Sea lice have also been observed on fish caught in recreational fisheries but no accessible compilation of this data exists.

Table 1: Production from aquaculture, round fish, tonnes – Iceland (FAO 2010)

Year	2009*	2008	2007	2006	2005	2004	2003	2002	2001	2000
Salmon	500	283	1 158	6 895	6 094	6 020	3 700	1 471	2 645	3 370
Arctic char	3 200	3 006	2 145	1 426	977	1 336	1 670	1 540	1 320	1 364
Rainbow trout	100	0	10	10	50	142	180	248	105	95
Halibut	50	19	31	141	129	123	95	120	93	30
Turbot	80	41	70	47	115	62	32	9	3	0
Cod	1 200	1 502	1 467	1 412	1 050	595	445	205	70	11
Total	5 130	4 851	4 881	9 931	8 415	8 278	6 122	3 593	4 236	4 870
	*Estim	ated								

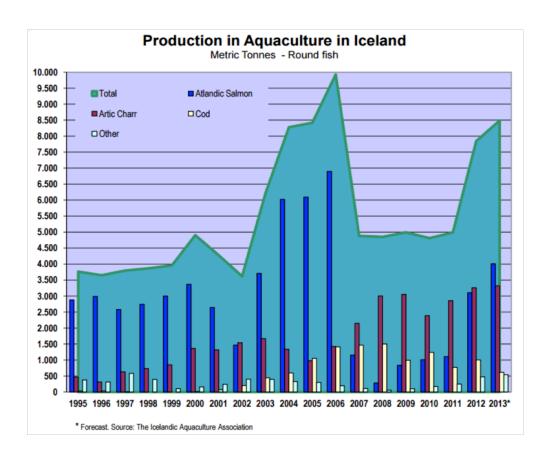


Figure 3: Production of fish in Icelandic aquaculture in tonnes from 1995 to 2013. Species shown are the main three species and all other species are grouped together in "Other". (The Icelandic Aquaculture Association, 2013)

Table 2: Data for lice counts carried out on fish in cages in Arnarfjörður operated by Fjardarlax. Number of fish sampled were 36 in August and 24 in September.

Date	L. salmonis Adult Female with Eggs	L. salmonis Adult Female without Eggs	L. salmonis Pre-Adult Female	L. salmonis Adult Male	L. salmonis Pre-Adult Male	C. elongatus Male & Female
29/08/2014	0	0	0	0	0	8
18/09/2014	0	0	0	0	1	44

Table 3: Data for lice counts done in farms in Arnarfjörður, operated by Arnarlax. Number of fish sampled were 25 in July, 17 in August, 20 in September and 19 in October.

Date		L. salmonis Pre-Adult I-II		C. elongatus
23/7/2014	0	0	1	0
12/8/2014	1	0	0	0
03/9/2014	0	0	0	11
23/10/2014	1	0	0	29

1.4 History and current situation of sea lice

The term sea lice is applicable to many different parasitic organisms in the ocean. As this variety of organisms has plenty of different hosts it has to be further specified that the sea lice that are important for this study are only two different organisms with the focus being on one of them. This is the so called salmon louse *Lepeophtheirus salmonis* Krøyer while the other one is often referred to as fish louse, *Caligus elongatus* Nordmann. The salmon louse has been in the focus of research for a while now and the first description most likely dates back to the 18th century. Here the Danish-Norwegian bishop Erik L. Pontoppidan described the following:

'great schools of salmon moving from the sea into fresh water, partly to refresh themselves, and partly to rid themselves by rubbing and washing in the swift currents and waterfalls, of a kind of greenish vermin called 'Laxe-Luus,' attached between the fins, plaguing it in the heat of spring' (Berland & Margolis., 1983).

Considering that nowadays the focus lies on negative impacts of sea lice it seems unreasonable that salmon lice had once been considered a sign of prime quality. This was due to the fact that it showed a recent entry into freshwater and thus the decline in quality, which is inherent to sexual maturation, could be excluded (Torrissen et al., 2013). Both, L. salmonis and C. elongatus occur naturally on salmonids (Thorstad et al., 2014). Main host species for L. salmonis in Northern and Western Europe are salmon, sea trout and Arctic charr (Pike & Wadsworth, 2000). It has a circumpolar distribution in the northern hemisphere (Boxaspen, 2006) and to date has been recorded on 12 different salmonid species (Pike & Wadsworth, 2000) with only very rare examples of other host species (Kabata, 1979). Due to the international focus on this parasite it can be considered the most studied sea louse species (Thorstad et al., 2014). C. elongatus has also been studied but not as intensively as L. salmonis as it is not host specific to salmonids but has been recorded on more than 80 different fish species throughout the world (Kabata, 1979). Unlike L. salmonis, C. elongatus can also be found on the southern hemisphere (Boxaspen, 2006) which is why southern countries with aquaculture like Chile focus monitoring and research on the *Caligus* species.

Heavy infestations with salmon lice have been observed on wild sea trout in Norway, Scotland and Ireland since the late 1980s (Bjørn, Finstad, & Kristoffersen, 2001; Butler, 2002; Gargan, Tully, & Poole, 2003). Clear impacts of sea lice on wild salmon and trout fisheries have also been observed (Torrissen et al., 2013). Those two things have been connected to increasing farming industry in these areas, as areas in the same countries that don't have farming activity do not show these trends (Butler, Watt, & Mills, 2003; Gargan et al., 2003; Heuch et al., 2005). Inside the aquaculture sector there have also been reports of disease problems starting around the same time period (Heuch & Mo,

2001). How this interaction between farmed and wild salmonids is perceived in the up to date literature will be explained later, but it can definitely be said that fish farming did not increase the geographic range of the salmon louse (Thorstad et al., 2014).

1.5 Aims

Iceland has an unique chance in providing data not only for its own aquaculture and wild fishery sector but also for those of other countries. While countries like Norway, Ireland and Scotland could just react to the problem of sea lice epizootics and had nearly no historical data from times before the start of intensive fish farming, the situation is different here. Salmonid aquaculture in Iceland in general, and in the Westfjords in specific, is a young industry considering that farms in the Westfjords have not been operating with salmon for more than two years. Data that is collected now, can substantially improve management and control of sea lice as it will show the natural infections rates and abundances on wild fish. By comparing areas with differing distances to these existing salmon farms it will be possible to determine if there is already an impact from salmon aquaculture on wild stocks. Sampling is based on gill netting, as this is a method which has been used in various other areas.

1.5.1 Research questions

The three research questions that this study will focus on are:

- 1. How high is the abundance of sea lice in the wild populations of salmonids in parts of Arnarfjörður?
- 2. Which developmental stages are present at which time?
- 3. Is there a significant difference between sites that are close and sites that are further away from existing salmon farms?

2 Literature Review

2.1 Overview

This part of the study will be used to thoroughly inspect the current knowledge and state of research about anything that could be of importance. First, it will focus on salmon and trout as the two species, which have been and are used in both recreational fisheries and aquaculture. It will then go to sea lice focussing on the present situation around the world, the biology and ecology of sea lice, the interactions between parasite and host population and the issues that are connected to sea lice infestations. Current sampling and monitoring methods as well as legislation that is in place are assessed. Following this part the focus will be put toward aquaculture, especially the costs that sea lice can cause in this sector and how sea lice infestations in this sector can impact wild salmonid populations. This literature review will be used to analyze the results of this study, according to the best knowledge currently present.

2.2 Wild salmonids

2.2.1 **Salmon**

Atlantic salmon, hereafter referred to as salmon, feed on various organisms. Prey for salmon is mostly compiled of insects, crustaceans and other fish (Keeley & Grant, 2001). How much each of these groups are preyed on by salmon depends on the habitat and the size of the salmon itself. Predators that prey on salmon can be classified into micro (bacteria, virus and parasites) and macro (birds, shark, seal etc.) (Frazer, 2008) but every one of these predators inflicts a different predation pressure on wild salmons. Similar to the prey of salmon, the predators also vary between different habitats and between the different sizes of salmon.

The life cycle of salmon has been studied intensively and it varies between anadromous and non-anadromous salmon. The latter is however not of interest for this study as it does not interact with sea lice at all, which lays the focus of this study on the former. Adult salmon enter the freshwater habitat typically between May to September

(Guðjónsson 1978) while the main run usually is in July. Spawning, which is the reproduction process of salmon, occurs in the month from September to December. Hatching of the eggs in the cold Icelandic rivers takes between 6 and 8 month and is mainly dependent on water temperatures (Guðbergsson & Antonsson, 1996). Salmon undertake their first migration to sea when they are between 3 and 5 years old (Mills, 1989). They stay at sea for various amount of times but mostly between 1 and 3 years (Guðjónsson 1978), before they return to the same river they hatched in and thus complete the cycle. Different then Pacific salmon the Atlantic salmon is iteroparous, meaning it can spawn repeatedly (Schaffer, 1974) even though adult fish do not always migrate out to sea again but die during the spawning process. The migration patterns between fresh- and seawater differ between populations of salmon and are likely to be various even inside one population (Randall, Healy, & Dempson, 1987). Smolts are observed to migrate out to sea, which means out of the rivers and the adjacent fjords toward the open ocean, swiftly (Davidsen et al., 2008; Finstad, Økland, Thorstad, Bjørn, & McKinley, 2005). They migrate because of the profitable feeding grounds in the open ocean (Gross, Coleman, & McDowall, 1988). While migrating, the salmon is typically travelling close to the water surface, the majority travels at a water depth of under 3 meters, and the shoreline (Sturlaugsson & Thorisson, 1995 & 1997). The heaviest mortality is connected to the first month after salmon have left the freshwater habitat due to osmoregulatory issues and a high predation especially on younger and less experienced fish (Hansen, Holm, Hoist, & Jacobsen, 2003). In order to minimize these negative effects, salmon smolts usually only start migrating at a certain water temperature of roughly 8 degrees Celsius or higher (Hvidsten, Heggberget, & Jensen, 1998; Thorstad et al., 2012). Salmon that have escaped from fish farms are also included in wild populations, and have been found to have a slower outward migration then other wild salmon (Hansen & Lund, 1992). More in-depth reviews of all aspects of this species have been conducted before and are accessible for further gain of knowledge (e.g. Jonsson & Jonsson, 2011; Mills, 1989)

2.2.2 Trout

Over 50 different species of trout have been described in the literature and they are all grouped in one polymorphic species (Behnke, 1986). The term sea trout is generally used for trout that have an anadromous life cycle and this is how it will be used here as well. Just like for salmon, non-anadromous populations are existent in various areas (Jonsson & Jonsson, 2011; Klemetsen et al., 2003) but are not of interest for this thesis and will thus not be touched by this review. Sea trout prey on similar organisms as salmon do (Klemetsen et al., 2003), and in turn also gets predated on by similar predators (Dieperink, Pedersen, & Pedersen, 2001). The main difference here is the lack of predation on the open ocean as trout does not usually migrate that far away from the coast, a process that will be explained in more detail. Trout reproduce in autumn or winter with the start of the spawning depending on latitude and altitude. An increase in one or both of these variables means an earlier start of the spawning procedure, due to the colder water temperatures and longer egg development times (Klemetsen et al., 2003).

Duration of freshwater residence differs a lot between populations and even inside one population. Sea trout smolts have been observed to stay in freshwater between 1 and 8 years (Jonsson & L'Abee-Lund, 1993) before they migrate to sea, feed and return for spawning. This is called a bet hedging strategy and it increases survival and population stability (Ellner & Hairston, 1994; Roff, 1992). After they have left the freshwater habitat they, in the northern latitudes, usually stay in the marine environment between 1 and 6 months to feed (Berg & Berg, 1989; Klemetsen et al., 2003). There have however, also been frequent reports of sea trout which overwinter in the marine environment or undertake sea migrations during wintertime (Jensen & Rikardsen, 2012; Olsen, Knutsen, Simonsen, Jonsson, & Knutsen, 2006; Pemberton, 1976; Rikardsen, 2004), which is thought to be due to harsh conditions in rivers and streams (Jensen & Rikardsen, 2012). These fish are also believed to be mostly immature, which keeps them from undergoing the upstream migration (Berg & Jonsson, 1990). Cases of immature trout returning to freshwater have also been reported and stand in connection to parasite infections (Birkeland, 1996). These fish lose out on the increased feeding

opportunities in the ocean but gain from loss of parasites and less osmoregulatory pressure (Birkeland, 1996). During their migration sea trout prefer shallow waters (Lyse, Stefansson, & Ferno, 1998) and rarely move further away from their respective spawning rivers than 100 kilometres (Berg & Berg, 1989, Klemetsen et al., 2003). Leaving the freshwater environment is similar to salmon, stressful for sea trout and a temperature dependent migration is highly likely due to the fact that low water temperatures delay smoltification (Hvidsten, Jensen, Vivås, Bakke, & Heggberget, 1995). Higher water temperatures are also preferable as the salinity tolerance is higher than in low water temperatures. Consequently in years with a late spring the migration period of sea trout is delayed (Bjørn & Finstad, 2002). Another trait of sea trout populations is the fact that more females than males actually undertake migration (Jensen et al., 2012; Solomon, 2006). The ratio for this behaviour is found to be around 1.5 (Jonsson, 1985). As for salmon, there are also in depth reviews about sea trout available (Elliott, 1994; Jonsson & Jonsson, 2011).

2.3 Sea Lice

2.3.1 Biology, ecology and influence on the host

In wild populations the abundances of salmon lice varies between host species, years and even individual fish from one population. The impacts that salmon lice can have on an individual fish are dependent on its species, as susceptibility to negative effects is different between species (Fast et al., 2002; ICES, 1997). Variations in natural salmon lice abundances are not completely understood but have been linked to changes in temperature and salinity (reviewed in Boxaspen, 2006). *L. salmonis* undergoes eight developmental stages, each of them being separated by a moult (Hamre et al., 2013) (**Figure 4**). A new filament which is used to attach to the host is produced for every moult (Gonzalez-Alanis, Wright, Johnson, & Burka, 2009).

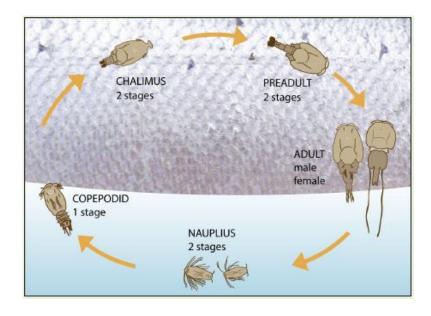


Figure 4: Life cycle of the salmon louse Lepeophtheirus salmonis, showing both free-swimming and attached stages. (from Thorstad et al. 2014)

The first two stages of the life cycle are planktonic, called nauplii and drift with the currents (Asplin et al., 2013; Boxaspen, 2006; Hamre et al., 2013) (Figure 4). Salmon louse thus have six post-nauplius instars which is generally the case for other sea lice and copepods. This fact has however only been shown in 2013 by Hamre et al., as prior to that the salmon louse was believed to have ten stages in total and eight post-nauplius stages (Johnson & Albright, 1991a). Hamre et al. (2013) showed that there are only two chalimus stages instead of four. Due to that, any literature about the life cycle of salmon lice dating from before this study has to be carefully read in order to not base anything on the initially proposed life cycle. Nauplii live on energy reserves and survival time is based on size of the larvae and temperature of the water column they drift in (Boxaspen, 2006; Costello, 2006). Movement is, however, not restricted to drifting, they have also been shown to actively move vertically through the water column (Costelloe, Costelloe, & Roche, 1995). Larvae are especially congregated in shallow estuarine areas (Costelloe et al., 1995) which can be explained in two different ways that can both contribute. First the horizontal movement with currents might place them in these areas and secondly ovigerous female detach from fish that are migrating upstream and the larvae hatch from eggs in the estuary (Costelloe et al., 1995).

With the moulting into the third stage, copepodid, the louse becomes infective (Hamre et al., 2013; Hayward, Andrews, & Nowak, 2011) and actively searches for a host to attach to (Figure 4). Frequent sites of attachment are skin, gills and other external surfaces, with the fins being especially important for the first attachment (Bron, Sommerville, Jones, & Rae, 1991). The infectious copepodid stage can develop at a wide temperature range (Jacobsen & Gaard, 1997) but there are differences in the rate of development (Heuch, Knutsen, Knutsen, & Schram, 2002). While larvae only need 8.7 day on average in water with 10 °C it will take them on average 45 days at 2 °C, effectively slowing down the whole life cycle (Boxaspen & Næss, 2000). Copepodids are able to sense changes in salinity levels, can endure low salinity situations and can supposedly actively move towards haloclines (Bricknell et al., 2006). Prior to attachment the copepodid entirely depends on endogenous lipid reserves and does not spend time foraging or feeding (Torrissen et al., 2013). Its only activity is the search for a suitable host and the attachment to that host. Survival time is about 7 days (Stucchi et al., 2011) but energy content and thus ability to attach to a host are diminishing between day 3 and 7 (Tucker, Sommerville, & Wootten, 2000). Multiple studies have been conducted on how far louse larvae can disperse in their life span of 5 to 15 days before they either find a host or die (Foreman, Czajko, Stucchi, & Guo, 2009; Murray & Gillibrand, 2006; Siegel, Kinlan, Gaylord, & Gaines, 2003). It has been shown by these studies that dispersal is on average 27 kilometres from the source with a total range of 11-45 kilometres. This is however, highly dependent on local hydrographic factors and can thus only be used as a guideline and not as exact values. Estimation of larvae dispersal is as of today done by using hydrographic models which use various factors like wind forcing or current speeds. A first feasability assessment for the use of such models was done by Karbowski (2015). Most likely connected to the on average low migration depth of salmonids, most copepodids concentrate within the top three meters of the water column during daytime and spread out towards slightly deeper depth at night (Heuch, Parsons, & Boxaspen, 1995; Hevrøy, Boxaspen, Oppedal, Taranger, & Holm, 2003). To allow an efficient search for a host, copepodids are equipped with certain traits. Evidence suggests that they can visually detect passing hosts from shadows and the flashing of scales (Pike & Wadsworth, 2000). They also possess

mechano- and chemoreceptors. The former allows for identification of vibrations which are produced through movements done by a nearby host (Heuch & Karlsen, 1997). An approximate distance to the host of 26 mm or lower is necessary for these receptors to detect signals (Heuch, Doall, & Yen, 2006). The latter is used by the copepodid to detect odours which are left by passing fish (Ingvarsdottir et al., 2002; Mordue & Birkett, 2009). Using this they can classify different fish in suitable and non-suitable hosts (Bailey et al., 2006). Once a suitable host has been found, by using one or multiple of these traits, the copepodid increases swimming speed and directs its movement towards the host (Genna, Mordue, Pike, & Mordue, 2005; Mordue & Birkett, 2009). The ability to attach safely to the host is thought to be affected by local current speed around the host fish (Bron et al., 1991). This makes the swimming speed of the host an extremely important factor for whether the lice can or cannot find attachment. A study was done by Genna et al. (2005) which showed that a slow moving host (swimming speed of 0.2 cm/s) allowed for a high number of attached lice whereas only a very small amount of lice could attach to a fast moving host (swimming speed of 15 cm/s). Once the copepodid moved close enough to the host it grips it with the second pair of antennae and maxillipeds (Costello, 2006).

After successful attachment the salmon louse can complete its lifecycle. The copepodid moults into two separate pre-adult stages and one adult stage either becoming female or male for these last three stages (Igboeli, Burka, & Fast, 2013) (Figure 4). They are often referred to as mobile stages as they are not restricted to their site of attachment but can move around the host and even switch hosts (Johnson & Albright, 1991b). Being able to move is very helpful for finding mating partners and especially for avoiding predation. It has been shown in studies that salmon lice, mostly males, leave their host fish when it is predated, a process that can result in as many as 70 percent of all lice transferring from this fish (Connors, Krkošek, & Dill, 2008). The mobile stages are designed in a way which allows them to be actively pressed to the host by surrounding water flow and their movement is powered by jet propulsion (Costello, 2006). In the mobile phase most lice redistribute on the fish, aiming for the head region and the ventral and dorsal midlines (Todd et al., 2000). During the whole attachment the louse

is actively feeding of the host fish, utilizing the hosts mucous, skin and blood (Brandal, Egidius, & Romslo, 1976). Rasping mouthparts are used to graze the host and feed on the material that is detached during this process (Costello, 1993). *L. salmonis* can produce secretory products like Prostaglandin E2 (Fast et al., 2004), a potent vasodilator, to protect themselves from immune reactions and create a good environment on the host (Fast, Johnson, Eddy, Pinto, & Ross, 2007). The skin of the host fish is the most vulnerable part and the parasite can cause different impacts. These are for example bleeding, tissue necrosis or altered mucous chemistry and they all negatively impact the host or even lead to the loss of physical and microbial protective functions (Costello, 2006). Host fish are especially vulnerable to secondary infections due to the open wounds caused by *L. salmonis* (Costello, 1993). More issues caused by the salmon louse will be named later.

After the last moult the salmon louse becomes adult and its only goal now is reproduction. The sexes can be distinguished by size and morphology with the female, 10 to 18 mm, being bigger than the male lice which only reaches 5-7 mm (Hayward et al., 2011, Pike & Wadsworth, 2000). Adult salmon lice are most resistant to changes in the surrounding environment thus they are able to for example overwinter on the fish in the open ocean (Heuch, Nordhagen, & Schram, 2000; Mustafa, Conboy, Burka, Hendry, & McGladdery, 2000). During the oceanic phase of the fish there is actually a recorded accumulation of adult sea lice on the fish (Jacobsen & Gaard, 1997). Females that have gone through the process of overwintering on their host are subsequently bigger than females that become ovigerous in the same year as they attached to the host (Costello, 2006). These females produce and release more eggs and these are also bigger than eggs from other females. Bigger eggs allow for an increased amount of food reserves for the hatching larvae and they can in turn remain planktonic for a longer time before they die, increasing the chance of finding a suitable host (Costello, 2006). A female louse can in general produce up to 11 clutches of eggs with each of those clutches containing between 200 to 800 eggs in paired strings which are attached to their abdomen (Heuch et al., 2000) (Figure 5). The first string of eggs that is produced by a female lice always carries less eggs then the following ones (Heuch et al., 2000). The mating procedure is done on the host fish most likely by using pheromones to attract a mating partner (Mordue & Birkett, 2009). Male salmon lice leave the female louse after mating to search for other females to mate with (Frazer, 2008). Completing a life cycle does not always take the same amount of time but is mostly temperature dependent as already mentioned. Additionally, there is also a difference between the two sexes as males take about 40 days to fully develop and females need approximately 10 days longer than that (Pike & Wadsworth, 2000). These numbers were recorded for a constant water temperature of 10 °C. Other studies confirm these development times and also show that even at constant temperatures not all lice develop at a similar speed (e.g. Finstad et al., 2007).



Figure 5: Adult female salmon louse with attached eggstrings (Source: Author)

If a fish enters into freshwater salmon lice do not immediately die (Costello, 1993). Other than *C. elongatus*, which only has a very limited survival time in freshwater, *L. salmonis* can survive for up to 14 days (Finstad, Bjørn, & Nilsen, 1995). This might be an adaption to hosts that frequent brackish waters. Eggs of both *C. elongatus* and *L. salmonis* do not hatch in freshwater and it is thus of high importance that ovigerous females keep their eggs in saltwater (Costello, 1993).

2.3.2 Interactions between host and lice populations

On a general level the risk of an infection with salmon lice is mainly determined by the infection pressure in a certain area and the time period that fish are exposed to

infectious lice (Heuch & Mo, 2001; Sivertsgård et al., 2007). When considering the individual level other factors are of importance like the size of the fish, the nutritional status and the stress level prior to the infection (Johnson & Albright, 1992; Jones, 2001; Tucker, Sommerville, & Wootten, 2002). A difference in resistance has been shown between populations of one species, for example sea trout. Both genetic variations and adaption have been named as reasons for those differences (Glover et al., 2003; Glover, Nilsen, Skaala, Taggart, & Teale, 2001, MacKinnon, 1998). The behaviour of salmon during their migration gives them an advantage over sea trout, as they migrate quickly out to the open ocean and reduce the chance of getting in contact with infectious salmon lice (Finstad et al., 2005, Klemetsen et al., 2003; Sivertsgård et al., 2007; Thorstad et al., 2007). This is called migratory allopatry (Krkošek et al. 2007). Infection can occur on the open ocean but as the area that salmon cover in that phase of their lifecycle is a lot bigger than a fjord, the infection pressure is reduced (Jacobsen & Gaard, 1997). Sea trout spend their life at sea mostly in close proximity to the shoreline (Aarestrup, Baktoft, Koed, del Villar-Guerra, & Thorstad, 2014; Middlemas, Stewart, Mackay, & Armstrong, 2009; Thorstad et al., 2014) and are thus exactly in those areas that salmon lice larvae have been shown to accumulate (Bjørn, Finstad, Kristoffersen, McKinley, & Rikardsen, 2006; MacKenzie, Longshaw, Begg, & McVicar, 1998). Amplification of infection levels is also very likely to happen in these habitats like fjords as both out and inward migrating fish are in close proximity (Torrissen et al., 2013). This can affect both salmon and trout. Studies by Copley et al. (2005) and Jackson et al. (2012) revealed the fact that lice on fish that are returning from their marine phase are mainly ovigerous females and that prevalence of lice on these fish is nearly 100 percent. While the risk for an infection is connected to the amount of infectious larvae, the chance of attachment that these larvae have is also directly dependent on the amount of host fish in the area. This will become important when looking into the increasing amount of salmonid aquaculture along the coastlines, but it always has to be considered that only one percent of all nauplii that hatch from one pair of egg strings have to survive to maintain the current population (Frazer, 2008).

Salmon lice are reported to have population regulating effects on their host fish (e.g. Jackson et al. 2011) which can be very significant and eventually lead to loss of populations if the amount of lice is high enough (Gargan et al., 2012; Krkošek et al., 2013). Fish that are infected with salmon lice can, for example, be easier caught by predators due to factors like decreased reaction times and swimming speeds (Grimnes & Jakobsen, 1996; Wagner, McKinley, Bjørn, & Finstad, 2003). Considering a completely natural ecosystem which is not influenced by anthropogenic factors, these effects should decimate fish populations until they reach a level where there are simply not enough fish anymore to sustain lice population. Following this, the lice population will shrink and the fish population can grow again (Frazer, 2008). Fish and lice population are thus, at least roughly, following the rules postulated by Lotka and Volterra which describe the relationship between predator and prey population (Volterra, 1926). Ultimately this should lead to a certain equilibrium between the two populations but such a thing does not exist in nature (Frazer, 2008). In reality this system is disturbed by many things, ranging from extreme temporal changes in weather to anthropogenic influences like aquaculture or fisheries which respectively increase or diminish the density of host populations (e.g. Bergh, 2007; Dobson & May, 1987). Host densities are in general very important as so called thresholds for lice epidemics can be estimated. According to Krkošek (2010b) epizootics can be prevented by keeping the host density below the approximated threshold. However, limitations to these thresholds exist and in the same study Krkošek (2010b) warned that thresholds can be crossed even when there are no changes in the host density due to, for example, shifting environmental factors. Infection pressures seem to be especially high at spring time, for example, as water temperatures rise and fish return from the ocean to spawn (Jackson, Deady, Leahy, & Hassett, 1997). Coinciding with this is a maximum in somatic size of adult female salmon lice, which is believed to increase fecundity (Jackson, Hassett, Deady, & Leahy, 2000).

2.3.3 Problems associated to sea lice infection

Taking specifics of the *L. salmonis* life cycle and their interactions with the host populations into account, it has to be said that evidence for negative impacts of sea lice

on their hosts do exist. These negative impacts can be various and the problems that the host fish can have due to those will be explained further. They have to be divided into lethal and sub-lethal issues. One of the first studies that showed direct lethal effects of salmon lice infection on wild sea trout populations was conducted in the Hardangerfjord in Norway (Skaala, Kålås, & Borgstrøm, 2014). Most studies however only showed sub-lethal effect, like for example increased protease activity in the host fish especially around the sites of infection, which hints at general biochemical changes in the host (Ross, Firth, Wang, Burka, & Johnson, 2000). Juvenile salmonids have been found to show an altered behaviour when newly infested with salmon lice. They tend to leap and roll more than they normally would, thus increasing the chance that predators become aware of their presence (Grimnes & Jakobsen, 1996). Sea trout that have a high number of salmon louse are also shown to spend more time close to the surface (Gjelland et al., 2014) which is believed to be a trade-off between less infection pressure and a higher risk of predation (Ward & Hvidsten, 2011). Sub-lethal infection levels always have to be considered very carefully, as they can alter the behaviour of the host and render it susceptible to secondary infections due to a modulated stress response of the host fish (Heuch et al., 2005; Nolan, Reilly, & Bonga Wendelaar, 1999). Levels of 0.1 lice per gram bodyweight and above can be considered pathogenic (Todd, Whyte, MacLean, & Walker, 2006; Serra-Llinares et al., 2014) and even though an exact number is hard to determine, countries with extensive salmonid aquaculture have included maximal infection levels into their legislation.

The skin of the host fish, and other parts that are in close proximity to the attachment site of the lice, are especially vulnerable to lice induced damage. The external layers of a fish are very important as they work as a barrier for infections and are part of the osmotic system which allows the fish to control the salinity of internal tissues (Frazer, 2009). Lice infections can cause necrosis of skin cells, increased mucous discharge and similar effects which can be amplified by the increase in stress levels of the host fish (Costello, 2006; Nolan et al., 1999). In general it can be said that the skin damage that is caused by salmon lice is proportional to the size of the lice. While the copepodid stage is only able to cause minimal skin damage the bigger stages like adult males and

females can lead to a significant disturbance of the outer tissues (Pike & Wadsworth, 2000; Thorstad et al., 2014). A study by Dawson (1996) showed that fish with more than 100 copepodids attached did not suffer from reduction of physiological performances. The already mentioned study by Skaala et al. (2014) showed that around 80 or even 90 percent of all sea trout that were returning to a river had fin damage that was evidentially caused by salmon lice. Future studies on lice ecology, life cycle, distribution and degree of negative effects need to be conducted as a lot of the projects that have been used as sources for this literature have not, or only in a small amount, been replicated. They can be used to predict certain effects of increased fish farming but generalising or validating them for all areas should not be done.

2.3.4 Sampling

In order to sample sea lice on wild fish different methods can be used. One that has been used for the most part of the current literature is gill-netting (e.g. Bjørn et al., 2010; Serra-Llinares et al., 2014.) With deployment of these nets wild fish have been captured so that numbers of sea lice could be counted and developmental stages could be assessed. This sampling method can be considered as the cheapest available option which does not need a lot of preparation in order to be used which made it a good choice for this study. There have however, been reports about the limitations of this method which are causing researchers to switch to other options if it is feasible. When fish get caught in one of the deployed gill-nets they will struggle to escape which can lead to detachment of sea lice (Thorstad et al., 2014). A measure that can be taken to reduce this effect is to lower the deployment time of the nets and check the deployed nets frequently and if possible even continuously (Bjørn et al., 2001). The amount of handling that is needed to free the fish from the net in order to kill and preserve it for later analyses is also quite high which can also cause loss of lice from the fish. Also, the fact that the fish have to be killed in order to analyze and count the sea lice is not ideal. While generally bigger sample sizes are preferred it has to considered not to take too many fish out of the wild populations to not cause negative impacts on those. Areas for sampling need to be chosen wisely and have to be inclusive enough in order to not cause a skewed data set (Bjørn et al., 2001). Other options that are used in recent studies

are, for example, other net variations which act like a stationary trap. These traps reduce the lice removal while maximizing the survival of the fish, possibly allowing the researcher to collect the lice of the fish and releasing it again (Barlaup et al., 2013).

2.4 Salmon Aquaculture

2.4.1 Appearance and the accustomed costs of sea lice in marine salmon aquaculture

Examples of sea lice induced problems in salmon aquaculture are manifold which is why only one will be given here. It is from the aquaculture sector on the Atlantic coast of Canada, in the Bay of Fundy (Hogans, 1995). In the time period from 1988 to 1993 there were no recorded problems with sea lice infections, the intensities were below 5 lice per fish. The following winter however was the start point for an epidemic outbreak of sea lice, as intensities increased to over 20 lice per fish and prevalence approaching 100 percent. This process created considerable losses for the aquaculture companies in that fish mortality increased, surviving fish had less market value and counteracting measures had to be taken. An estimate of the global scale of these losses due to sea lice infection was done by Costello (2009b) who named sea lice as the most pathogenic parasite. The estimate was about 300 million Euro every year and around 6 percent of product value. Treatment cost for western Canada were estimated to be around 0.08 to 0.11 US Dollar per kilogram of salmon in a cage (Mustafa, Rankaduwa, & Campbell, 2001). This estimate will however, most likely be outdated by today and even if it is not it should not be used for estimates of costs in other countries as they might use completely different treatments or the prices for the same treatment differ between the two countries.

2.4.2 Impacts on sea lice infestations in wild salmonid populations

As shown above, both wild and domestic populations of salmonids share parasites, with individuals of the parasite population being able to freely transfer between both host populations. This kind of transmission is called spillover and spillback of parasites and can be considered as an important mechanism for the beginning of an epizootic (Daszak, Cunningham, & Hyatt, 2000). If lice from wild fish attach to fish inside an

aquaculture farm they can quickly reproduce and their offspring has lots of viable hosts close by. As most aquaculture cages consist of a big fine meshed net with a floating part on top, lice larvae might even get trapped inside these cages as they are not dispersed due to constricted water flow (Costelloe, Costelloe, & Roche, 1996). This will lead to a staggering increase in the parasite population which can then spill back to the wild population causing higher infection rates than in a natural system without the aquaculture (Murray, 2008) as it has been shown for other parasites (Kent, 2000). Spillback might also be limited due to constricted dispersal of larvae but the amount of this effect is not known. Marine based salmonid aquaculture is located in close proximity to the shoreline and thus increases the host density in those areas which has to be taken into account for estimating possible thresholds. An example for this procedure comes from Pacific Canada where salmonid farming was started in 1987 with the first epidemic outbreak only occurring in 2001. This 14 year delay is thought to be due to fish farming increasing the host population until reaching and crossing the threshold (Krkošek et al., 2007). The time it took in this example can however, not be used as a guideline for other areas as both host and farmed fish were pacific salmon, a species that shows different reactions to sea lice infection then salmon or trout. As salmonid farms also produce salmonids year round, apart from fallowing schemes which are used in some locations, the possible production of lice can even occur in late winter and early spring, a time where wild fish are naturally scarce (Heuch & Mo, 2001; Stien, Bjørn, Heuch, & Elston, 2005). The annual sea lice epizootics, which have been especially linked to areas with a high amount of fish farms, have in the past already been blamed for the collapse of certain salmonid stocks in fjords and the coastal waters. An assessment based on data from Ireland, Scotland and both Canadian coasts revealed a reduction in structural integrity of wild populations due to a lowered amount of survival when all areas were combined (Ford & Myers†, 2008). Data from Norway, Ireland and Scotland showed that highest lice abundances could be observed in an area of approximately 20 to 30 km from aquaculture farms (Gargan et al., 2003; Middlemas, Fryer, Tulett, & Armstrong, 2013; Serra-Llinares et al., 2014).

Epizootics on wild salmonids have been reported from every country with a major salmon aquaculture. Plankton surveys in Scotland, for example, showed that lice larvae mainly stemmed from adult females attached to farmed salmon (Penston & Davies, 2009). Displaying a similar trend was a study conducted in Ireland which showed that only 3.4 percent of fish in bays without fish farming had lice amounts above a critical level, while the amount of those fish in bays with fish farming, was as high as 31 percent (Gargan et al., 2003). Trends in Norway are consistent with this result, as infestation was significantly different between areas which are either exposed or unexposed to salmon farming (Bjørn & Finstad, 2002). Another way that salmonid aquaculture can impact sea lice infestations is by fish escaping from the farms. If these fish are infected with sea lice they immediately increase the parasite population (Heuch et al., 2005), especially in the immediate vicinity of the farm as they have been found to stay around it for a couple of weeks post-escaping (Hansen & Lund, 1992). With all these negative examples it seems mandatory for the Icelandic salmonid aquaculture industry to take all possible measures to prevent epizootics of sea lice. It has been postulated that this can be achieved by keeping track of the amount of expansions in an area (Frazer, Morton, & Krkošek, 2012). In combination with other measures, like hydrographic models to understand larvae dispersal and estimation of host thresholds, this might lead to a state where an outbreak never occurs and wild populations do not suffer from infections induced by fish farming.

2.4.3 Treatments

Due to the fact that sea lice problems have been known inside the aquaculture sector for quite a while now, there are already different treatment methods, with more being developed. As this is not the main focus of this thesis, only a few will be named which could potentially be used in Iceland as well. Fishing for escapees is proposed in certain areas during times when wild fish are either mostly in their freshwater habitat or out at sea (Skilbrei, 2005 cited in Boxaspen, 2006). As long as no members of the wild population are killed during this procedure it is a viable method to reduce the input of sea lice to the coastal waters. Chemicals can also be used but possible non-target effects are a common point of critique and in the year 2008 there was only one substance,

emamectin benzoate which was allowed to be used in all jurisdictions (Burridge, Weis, Cabello, Pizarro, & Bostick, 2008). One method which has become popular over the years is the use of cleaner fish. These specific fish are put into the cages together with the salmon and they actually use the lice that are attached to the salmon as feed. While doing so they remove the big lice, so the adult stages first, and thus immediately reduce the infection pressure by eliminating sea lice eggs (Treasurer, 2005). While wrasse have been the most used species, the possibility of using other species such as lump fish is being researched and the results are promising (Imsland et al., 2014).

The mentioned genetic differences between different salmonid populations could be used as an advantage by selectively breeding fish that show a high resistance to sea lice infections (Kolstad, Heuch, Gjerde, Gjedrem, & Salte, 2005). These fish could then not only be used in aquaculture but also in those areas where rivers are actively stocked for recreational fishing. Measures which are already used in aquaculture farms are fallowing, single-year productions and the removal of injured fish. While these are mostly taken regarding some other problem, like excessive nutrient input to the sea floor, they are also helpful to prevent sea lice epizootics. Just in order to show that not all methods from around the world would make sense in Iceland, an example from Japan can be used. Salmon farmers practice a very short grow-out period which does not allow sea lice to complete their life cycle more than once which prevents epizootics (Nagasawa, 2004). Iceland however has much lower sea temperatures which leads to lower growth rates of the salmon and if short grow out periods would be used the salmon would not be able to reach a marketable size.

2.4.4 Legislation

Being the country with the highest production numbers of farmed salmon, Norway has a network of regulations and laws in order to control sea lice levels in fish farms. Sea Lice counts are mandatory and have to be reported either every week or every second week depending on the sea temperatures. Lice are put in three different groups for these counts, sessile, mobile and adult female and averages of these three groups are reported (Revie, Dill, Finstad, & Todd, 2009; Jansen et al., 2012). Treatment has to be done by

the companies if on average more than 0.5 adult females or 3 mobile lice per fish are found during the summer period. In the winter period these numbers move up to a maximum of 1 adult female or 5 mobile lice on average per fish (Torrissen et al., 2013). Norway is also using protected zones trying to protect wild salmonid populations from a too high infection pressure and the negative effects which follow (Aasetre & Vik, 2013). Protected zones can either limit the amount of salmon farming or completely restrict it for a certain fjord or an even bigger area (Heuch et al., 2005). It has been suggested that these protected zones are too small to work effectively and either need to be extended or the farms surrounding them must also be limited to reduce the infection pressure on a bigger spatial scale (Bjørn et al., 2011; Heuch et al., 2005).

3 Methodology

3.1 Research sites

The research that builds the base for this project was conducted in Iceland, in the region that is called the Westfjords (Figure 6). All three research sites were located in the fjord system of Arnarfjörður. These sites were chosen for a number of different reasons. Firstly there is an already existing use of the area for salmon aquaculture, more specifically there are two locations, which are approximately six kilometres apart from each other. This distance is measured considering the usage of a boat. One of them, which is owned by Arnarlax, was, during the time of the research, at a capacity of 500.000 salmon, while the other one, which is owned by Fjardarlax, was holding 1.000.000 salmon. Secondly the area was pre-evaluated regarding the suitability for the gill-netting method which will be explained in section 3.3. Thirdly it was confirmed by local residents who were spending time doing recreational rod fishing in the area that they had been catching salmonids at those spots. One research location was located in the bottom of Fossfjördur, in close proximity to one of the two aquaculture sites and will in this thesis be referred to as Location A. A second one, which will be referred to as Location B, was located between the two aquaculture sites at a spot called Hjalli. A third, which will be referred to as Location C, was considered to be the control site, as it was the furthest away, approximately 8,5 kilometers by boat, from both aquaculture sites. The fjord in which this site was located is called Trostansfjördur. In all three spots the owners of the land adjacent to the research sites were contacted to inform them about the project and its goals. Some recreational rod fishing was observed during the project but no boats were seen in the immediate surroundings of the nets at any point. An overview of the three sites, the location of the two aquaculture sites and Arnarfjörður is given in **Figure 7**.

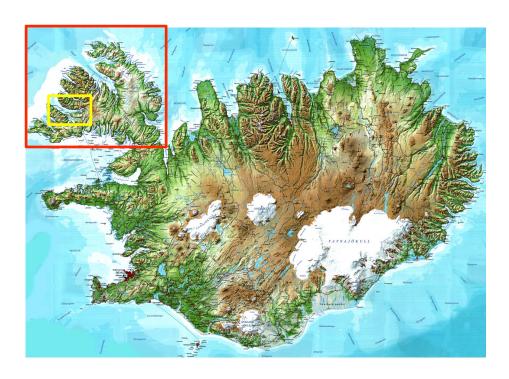


Figure 6: General map of Iceland showing the Westfjords inside the red and Arnarfjörður inside the yellow box. (Extreme Iceland, n.d.)



Figure 7: Detailed map of a part of Arnarfjörður in the Westfjords of Iceland. The three sampling sites are shown as well as the two already existing aquaculture farms. The green square represents the location of the net pens owned by Arnarlax, while the blue square represents the location of the net pens owned by Fjarðalax. Study site A, yellow indicator, is located in Fossfjördur, study site B, orange indicator, is located in Hjalli and study site C, red indicator, is located in Trostansfjördur. (Source: Google Maps, edited by Author)

3.2 Research period

The research was conducted in the month July, August and September 2014. Preevaluation of the sites and preparation of the project started in May of the same year. This time frame was chosen because it matches the stage in which anadromous fish can be found in the waters of the ocean and thus be sampled using the gill-netting method. Weather conditions are also formidable for field research during these month.

3.3 Pre-evaluation

Pre-evaluation was carried out in May, in cooperation with two experts from Norway, who are involved in the ongoing sea lice research there. The Pre-evaluation was done in two stages. At first the area was analyzed just using visual parameters. Different parts of the coast line in Arnarfjörður were visited with the two experts. It was made sure that all places which were then considered suitable for the gill-netting had a good habitat for anadromous salmonids. This was the case if a mixture of big to medium size rocks and large patches of seaweed were present. There being a not to steep depth gradient of the sea was considered necessary in order to confirm the suitability of an area. This was the case because it allowed the use of a maximum of 25 meters of rope at the off-shore side of the gill-net and allowed practical storage and transport on the boat. This pre-selection process chose three suitable sites for the project. Two of them, the one in Hjalli (site B) and the one in Fossfjördur (site A), were then used for test runs of the gill-netting method. Each site was tested once for the duration of one tidal cycle. The gill-netting method which will be described in section 3.4 worked in both of these sites. Four salmonids were caught in Site A during this trial run and one salmonid in Site B. The results of those two trial-runs were not included in any analysis. The third site that was selected during the pre-evaluation process was located in Hrafnseyri. This site was not used in the project because it was too far away from the place where the boat was located. In exchange for this, the Site C in Trostansfjördur was chosen as a control site, as it was closer and easier accessible. No trial-run was carried out for this site.

3.4 Gill netting

The gill-netting method which was used in this project was carried out, based on a similar methodology which is used in Norway. The desired sample size per site and month was 25 to 30 fish. One site was sampled continuously but due to bad weather or the lack of fish caught in the nets sampling was restricted and the desired sample size could not always be reached. In those cases the minimum amount of fish needed was set to 20 per site and month. Sampling was done over the duration of at least one low tide. The tidal times where checked every evening on a website, in order to determine the start of the sampling on the next day (United Kingdom Hydrographic Office, n.d.). If possible the nets were brought out around 1.5 to 2 hours before low tide but never later then at the point of low tide. In order to assure a safe sampling the weather forecast was checked every day prior to departure. Wind direction and wind speed were the main focus here and sampling was only started if these were not exceeding a certain frame of values. Sampling was carried out for at least 4 hours every time but in most cases the sampling time was around 6 hours. In some cases where it was feasible in regard to daylight and weather sampling was continued for another low tide cycle. In these cases the nets were left in the sea for at least 12 hours. Two different mesh sizes were used for catching the salmonids with one of them being 21 mm and the other one 26 mm. The gill-nets were 25 meters long and 2 meters deep, with a floating part on the top and a sinking part on the bottom which allowed them to stand vertically in the water column (Figure 8). Before the nets were dropped in the water a weight and a buoy were attached to both ends of the net (Figure 8). Each weight was a chain composed of metal links and weighed approximately five kilograms. The buoys were attached, using a rope with a length of 1.5 meters and were used to indicate the position of the net in the water. This made it possible to recognize the net even in bigger waves. The weight that was attached to the onshore side of the net was fastened with a 2 meter long rope, while the offshore weight was fastened with a 25 meter long rope. The weights worked well in all cases and allowed the nets to stay in the position that they were brought out in.

For this research two different boats were used. One of them very frequently and the other one only if it was available and in rougher weather conditions. The latter was a hard plastic boat, equipped with a 15 horsepower motor and was approximately 4 meters long. The boat that was used more frequently was an inflatable rubber boat from Quicksilver, equipped with a 25 horsepower motor and was approximately 3 meters long. There was no difference in the methodology due to which boat was used.

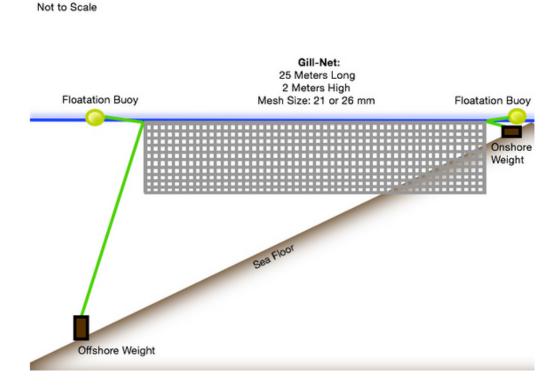


Figure 8: Schematic drawing of a deployed gill-net like it was used for this research. (Source: Author)

The start point for every day of sampling was in the bottom of Fossfjördur, where the boats were located. Before every single day of research the nets were prepared onshore. They were folded separately and placed in plastic buckets. A maximum of three nets per bucket allowed easy access and only a small amount of time was needed to bring them out. The buckets and the weights and buoys which were already attached to their respective ropes were placed in the boat together with a cooling device, plastic bags, labelling tags for those bags and knives. 5 nets were used for every day of sampling. They were brought out one after each other which took approximately 20 minutes. In

order to place them in an appropriate position and allow for good catch possibilities a certain technique was used for every net. The shoreline was approached with the boat head on, as close to the waterline as possible. The onshore side of the net was cast out including the attached buoy and weight at the estimated low tide line. The boat was then reversed which dragged the net out of the bucket. During this process it was made sure that the net did not get entangled in itself and was standing vertically in the water column. When the net was fully dragged out the offshore weight and buoy were attached and cast over board. It was checked if the net was positioned in an approximate 90 degree angle to the shore line and was not entangled in itself (**Figure 9**). If that was not the case the offshore weight was pulled up again and the net repositioned by manoeuvring the boat. This procedure was repeated for all 5 nets. The distance between the single nets varied slightly for the different sampling sites, but was never lower than a 100 meters. After being placed in the sea the nets were patrolled continuously using a boat to move from net to net.



Figure 9: Image of a gill net after deployment. The two buoys can be seen as well as the floating part of the gill net in between them. The rope leading to the attached weight can be seen below the buoy on the left side. (Source: Author)

In order to minimize the loss of lice from any fish that became entangled in the nets the maximum amount of time between every single patrolling run was one hour. The net was approached from one side, ideally heading into the current in order to prevent the boat, and especially the motor, from drifting into and getting entangled in the net. Every net was monitored visually until an entangled fish was discovered. If that happened the net was approached at the spot of entanglement. The net was cautiously taken out of the water in that spot assuring that the fish could not escape out of the net during this process. A small knife was used to cut the fish loose while the handling time of the fish itself was always as short as possible to prevent lice getting lost. The fish was then immediately euthanized by a blow to the head and placed in a plastic bag. The immediate surroundings of the entanglement spot in the net were checked for any lice that could have been detached from the fish. The same thing was done with the knife

and the gloves. If a lice was found in one of those places it was carefully detached from there and placed in the plastic bag together with the fish. Every bag was then equipped with a label which showed the date, the site and the net number. All plastic bags were kept in a cooling device on board of the boat and transferred to the lab as soon as the fishing was done for the day.

In order to take the nets in after the fishing for the day was done, the onshore buoy was approached by boat. It was hauled in together with the weight and both were detached from the net and placed in the boat. The net was then continuously dragged in the boat and placed in the plastic containers. Seaweed that was stuck to the net was removed, as much as possible, on site. After the whole net was stored in the boat again the offshore weight was dragged in, detached from the net and placed in the boat. All fish that were caught in one day of fieldwork were analyzed in the lab right away.

3.5 Lab analysis

To analyze the amount of lice per fish and the life cycle stages of those lice the fish were brought to a lab. They were analyzed individually using the following procedure for each fish. The information from the label were written down in the lab book and the fish was cut out of its bag. It was then placed in a container with water and the whole body was searched thoroughly for any lice. In order of making this search as effective as possible a flashlight was used which made it easier to spot the lice on the fish. Every fin was moved to be able to check the skin underneath. Each lice that was found on the fish was put on a glass tray using tweezers to detach them from the fish skin without damaging the lice itself. After all found lice were detached the plastic bag was checked as well for lice that had fallen of the fish during the storage and transport. These were then also placed on the glass tray (Figure 10). The glass tray was then placed under a microscope which was used to determine the species and life cycle stage of each individual lice. This was done using a 20-fold magnification. The amount of lice for the entire fish, as well as information about species and life cycle stage for each individual lice, was documented in the lab book. After the identification process all the lice were placed in a glass vile containing a 10-percent solution of Isopropanol. This conserved

the lice for any possible further analysis at a later stage. The fish was then measured and weighed and this data, as well as the species of the respective fish, documented in the lab book. The measuring scale that was used had an accuracy of 0,01 grams.



Figure 10: Several sea lice shown on the glass tray which was used for observation under the microscope. All lice shown here are sampled from the same fish. (Source: Author)

3.6 Sea lice stage identification

Sea lice were identified visually based on specific characteristics, which are displayed in the EWOS sea lice identification key, which was developed in the 1998 National Strategy for Sea Lice Control. These specific characteristics were also based on detailed identification characteristics discussed in the Schram (2004) article *Practical identification of pelagic sea lice larvae*. Identification was done in collaboration with a study on sea lice abundance and hydrodynamic modeling feasabiltiy during the same period in the same area (Karbowski, 2015) and was consistently used throughout the two studies. For each life cycle stage these specific characteristics can be described to differentiate between *Lepeophtheirus salmonis* and *Caligus elongatus* as well as between each specific life cycle stage within each species.

Nauplius 1 are small almost entirely clear or translucent and can be identified based on the colour and location of pigmentation. Nauplius 1 of *L. salmonis* are characterized by

black pigment which is visible around the eyes, dorsally and posteriorly as well as brown pigment which is found in the middle and evenly on both sides of the cephalothorax with all appendages lacking pigmentation at this stage. Nauplius 1 of *C. elongatus* are distinctly different from *L. salmonis* identifiable by the red pigment located on the anterior and on the ventral surface of the cephalothorax as well as a dark red pigment along the sides and posterior end (Schram, 2004).

Nauplius 2 are slightly larger, oval and slender still appearing translucent and can be identified based on the colour, location of pigmentation and shape of the cephalothorax. Nauplius 2 of *L. salmonis* are easily identified by black pigment around the eyes as well as posteriorly in bands across the cepholothorax and two distinct brown pigmented C-shaped figures located centrally on each side in the middle of the cepholothorax, appendages still lacking pigmentation (Schram, 2004).

Copepodids are again slightly larger, oval and slender in shape with pigmentation beginning in the cepholothorax and can be identified by the change in shape of the cepholothorax. Copepodids of *L. salmonis* are easily identified by two red eyes, a cepholothorax which is pointed at the anterior end, widest at the middle and a narrow somewhat pointed posterior end, with distinct C-shaped dark brown pigmentation. Copepodids of *C. elongatus* are easily identified by dark red eyes, a cepholothorax which is widest just above the middle, two distinct notches at eye level and near the anterior of the cepholothorax and 3 distinct patched of red pigmentation (Schram, 2004).

Chalimus 1 are again slightly larger, elongating vertically and the first visual sign of a frontal filament is evident (Costello, 2006). Chalimus 1 of *L. salmonis* are easily identifiable from other L. salmonis life cycle stages and from *C. elongatus* by a series of characteristics. The identification characteristics which distinguish Chalimus 1 L. salmonis from Chalimus 1 *C. elongatus* are the red eyes located mid-cepholothorax, the wide cepholothorax shape, pronounced frontal filament and lack of frontal notch near the eye level of the body. The identification characteristics which distinguish Chalimus

1 *L. salmonis* from Chalimus 2 *L. salmonis* are the longer but narrower frontal filament and lack of posterior cepholothorax segmentation (Schram, 2004).

Chalimus 2 are again slightly larger, elongating vertically as well as widening midcepholothorax. At this stage the identification characteristics which differentiate *L. salmonis* from *C. elongatus* are easily to distinguish. Chalimus 2 of *L. salmonis* are identifiable from Chalimus 1 due to a visibly distinct posterior cephalothorax segment, widened cephalothorax, lines extending the posterior cephalothorax segment up to the eye level vertically along the cephalothorax, as well as extended narrow fourth legbearing segment. Chalimus 2 of *C. elongatus* are much smaller than Chalimus 2 of *L. salmonis*, they are easily distinguishable from other life cycle stages of *C. elongatus* by the beginning stages of a posterior cephalothorax segment and increasingly pronounced frontal notch located just above the eyes (Schram, 2004).

Chalimus 3 of *C. elongatus* are significantly bigger than Chalimus 2 of *C. elongatus*. Chalimus 3 are also easily distinguishable by their pronounced frontal filament, pointed anterior of the cephalothorax, extended posterior cephalothorax segment and elongated fourth leg-bearing segment. Chalimus 4 of *C. elongatus* are significantly bigger than Chalimus 3 of *C. elongatus*. Chalimus 4 are also easily distinguishable by their widened cephalothorax, pronounced frontal filament, pronounced frontal antenna, developed posterior cephalothorax segmentation and a circular bulge to the posterior cephalothorax segmentation, narrowing near to the fourth leg-bearing segment (Schram, 2004).

L. salmonis has 2 pre-adult life cycle stages for both males and females which are larger, distinctly wider with a round shape cephalothorax and have a flat shape cephalothorax with red pigmentation. Male pre-adult 1 are easily identifiable by four distinct bump-looking characteristics on the anterior of the cephalothorax by the frontal plates, a wide and round shape cephalothorax, red pigmentation which has not progressed to dark red and along the fourth leg-bearing segment, genital complex or abdomen, without any distinguishable characteristics. Male pre-adult 2 are easily identifiable by two distinct bump-looking characteristics on the anterior of the cephalothorax by the frontal plates, a wide and round shape cephalothorax, a darker red

pigmentation and a distinctly short fourth leg-bearing, genital complex and abdomen segment, with two visible lines located vertically. Female pre-adult 1 are easily identifiable by a slightly narrow anterior cephalothorax, a wide mid to lower cephalothorax and red-orange pigmentation and a distinctly short posterior with a slight pointing down and outwards of the bottom edges of the genital complex. Female pre-adult 2 are easily identifiable by two distinct bump-looking characteristics on the anterior of the cephalothorax by the frontal plates, a wide and round shape cephalothorax, a darker red pigmentation and an enlarged genital complex and abdomen, with more developed and large pointing of the bottom edges of the genital complex (Schram, 2004).

L. salmonis and C. elongatus both have 1 adult life cycle stage for both males and females. The male and female adult stage of L. salmonis is easily distinguished from the male and female adult stage of C. elongatus by the larger size, much darker red pigmentation and flat shape cephalothorax. The adult male L. salmonis is identifiable by dark red pigmentation and round shape cephalothorax and a very distinctly shaped genital complex, which is narrow at the front of the genital complex then extending to a rounded and wide mid genital complex and again narrowing at the end of the genital complex. The adult female L. salmonis is identifiable by a very dark red almost brown pigmentation, very large genital complex, which has four distinct circular characteristics and developing or developed egg strings visibly extending from either side of the genital complex. The adult male C. elongatus is identifiable by an oval shape cephalothoax, light orange cephalothorax colour with red spotting over it entirely, distinct mid-cephalothorax lines the same on both sides of the cephalothorax, a wide and large upper genital complex segment and very distinct frontal plates extending out of the middle of the cephalothorax curving outwards along the cephalothorax. The adult female C. elongatus is very similar to the adult male only larger, with a developed and large genital complex and developing or developed egg strings visibly extending from either side of the genitical complex (Schram, 2004).

3.7 Cleaning of the nets

Nets were cleaned in the same facility where the lab was. Two methods of cleaning, manual and mechanical, were used depending on how dirty the net and which kind of dirt it was. First one end of the net was attached to an approximately 1,80 meter tall coat stand. The other end was placed on the ground in some distance away. Each net was then, stretch for stretch, picked up off the ground and cleaned. If there were any parts of seaweed attached they were taken off by hand and placed in a container to be thrown back in the sea at a later point. After all the seaweed was cleaned of from one stretch, the high pressure washer was used coarsely to get rid of other bigger particles stuck to the net. When one stretch was processed like that it was coiled on the coat stand. This procedure was repeated until every part of the net was placed on the coat stand. The net was then bundled and fixated on bottom and top. Using the high pressure washer all the remaining dirt was then cleared off from the net bundle. After this each net was taken from the coat stand and hung up in order to dry. Every net was left to dry for at least 24 hours before it was used again. During the cleaning process the nets were frequently monitored for any holes that originated from cutting fish out or the net getting stuck in rocks on the sea floor. Any net that was found to have a too high number of holes was discarded and not used in the research again.

3.8 Statistics

The Microsoft Office program Excel was used to do basic analytics of the gathered data. These included calculating total fish and lice numbers as well as values for prevalence, abundance and intensity as suggested by Bush et al. (1997). Prevalence was calculated by dividing the number of infected fish caught by the number of fish caught. Abundance was calculated by dividing the number of lice sampled by the number of fish caught. Intensity was calculated by dividing the number of lice sampled by the number of infected fish caught. For all other statistical analysis the program R was used. Kruskal-Wallis tests were performed to analyze the data, as it is also done in similar studies (Bjørn et al., 2006 & 2011). These tests were used to test for significance between the three sampling locations per month. This was done separately for all fish, for fish with a

body size smaller than 25 cm, for fish with a body size greater than 25 cm, for the salmon lice L. salmonis and for the fish lice C. elongatus. Differentiating fish by body size has been done in similar studies, for example by (Bjørn & Finstad, 2002). To test differences between the two size classes per month for all sites combined a Wilcoxon-Test was used. The level of significance in all these tests was p < 0.05. All graphics were created in R and exported from there in order to be put into this document.

3.9 Temperature and salinity data

The measurements for salinity and temperature were conducted on October 24th with a Conductivity Meter - Cond 3110 (WTW). Salinity in promill and temperature in degrees Celsius were recorded at each site at depth of 0.1, 1, 2, 3, 4 and 5 meters. The aquaculture site in Fossfjördur is constantly recording water temperature in degrees Celsius at a depth of 7 meters. This data was accessed (**Appendix 1**) and used for comparison in this study.

3.10 Limitation of the gill-netting and deviation from known methods

As this kind of research to the best of my knowledge has not been done in Iceland before, the methodology had to be adapted as there were some limitations. The time it took to get the project started and everything prepared was longer than initially planned which only allowed for two month of data collection and a relatively small sample size for the first site in the first month of sampling. In order to be able to collect data even on days with not so good weather the use of a bigger and more stable boat is suggested for any continuous research. This will also allow for the use of more nets at once as they and their respective weights can be stored on board easier. One limitation that became obvious during this research is the presence of mackerel. During a mackerel run through the fjord it was not possible to fish in the early morning and the evening hours because too many of those mackerel got entangled in the nets. The main problem with this is that a big amount of fish entangled in one net at the same time weighs this net down and diminishes the potential of catching any more fish which could be valuable for the

research. Also, if not controlled immediately many of those entangled mackerel will die in the net which is against the aim of this research to protect wild fish stocks. Another limitation which had a similarly negatively effect on the efficiency of the data collection was the high abundance of jellyfish. This was especially observed in the beginning of field work in June and early- to mid-July. Something that should have definitely been done earlier in the process of this study is the collection of salinity and temperature at the sampling sites. This would have allowed for a more detailed analysis of the site specific values and could have been of great value when trying to determine the duration that one life cycle of *L. salmonis* has in this fjord system.

4 Results

During this study a total amount of 175 fish was caught. Five of those were caught during trial runs in July and ten in September, with the rest being caught in July and August. In July a total of 78 fish were caught out of which 18 were caught at Site A, 24 at site B and 36 at Site C (**Table 4**). In August the total amount of caught fish was 82 with 28 at Site A, 25 at site B and 29 at Site C (**Table 4**). Out of the 160 fish caught in July and August 155 were sea trout, 4 were salmon with one of those being a Pacific salmon and one was a charr. All following results will be for the month July and August. A total amount of 801 sea lice were counted on the 160 caught fish. Sixty seven of these sea lice could not be identified which represents 12 percent of all sampled lice. The other sea lice were either *L. salmonis* or *C. elongatus* with total abundances of 660 and 101 respectively.

The lowest prevalence (ratio of infested fish per sample) was recorded at Site A in July with 0.706 while the highest was 1 at site B in August. Prevalence increased from July to August at all three sites (see **Table 5&6**). Abundance (mean number of lice on all fish per sample) was also lowest at site A in July with 3.471 and highest at Site B in August with 7.520. At all three sites the abundances were higher in August than in July (see **Table 5&6**). Lowest intensity (mean number of lice on all infested fish per sample) was 4.043 at site B in July and the highest was 7.520 at Site B in August. Intensities were higher in August than in July for all three sites (see Table **5&6**).

Table 4: Numbers of fish sampled per month and study site.

	Site A	Site B	Site C
July	18	24	36
August	28	25	29

Table 5: Values for prevalence, abundance and intensity for the month of July at all three sampling sites. Prevalence represents the ratio of infected fish in the sample, abundance represents the mean number of lice of all fish that were sampled and intensity represents the mean number of lice per infected fish that was sampled. Values for all fish caught at the site as well as values for fish smaller than 25 cm and larger than 25 cm are included.

July		Prevalence	Abundance	Intensity	
	Site A		0.667	3.471	4.917
		< 25 cm	0.625	3.625	5.800
		> 25 cm	0.700	3.000	4.286
	Site B		0.958	3.875	4.043
		< 25 cm	1.000	1.000	1.000
		> 25 cm	0.955	4.136	4.333
	Site C		0.778	3.889	5.000
		< 25 cm	0.692	2.462	3.556
		> 25 cm	0.826	4.696	5.684

Table 6: Values for Prevalence, Abundance and Intensity for the month of August at all three sampling sites. Prevalence represents the ratio of infected fish in the sample, abundance represents the mean number of lice of all fish that were sampled and intensity represents the mean number of lice per infected fish that was sampled. Values for all fish caught at the site as well as values for fish smaller than 25 cm and larger than 25 cm are included.

August		Prevalence	Abundance	Intensity	
	Site A		0.857	4.571	5.333
		< 25 cm	0.769	3.846	5.000
		> 25 cm	0.933	5.200	5.571
	Site B		1.000	7.520	7.520
		< 25 cm	1.000	8.333	8.333
		> 25 cm	1.000	7.409	7.409
	Site C		0.966	6.655	6.857
		< 25 cm	0.875	8.625	9.857
		> 25 cm	1.000	5.905	5.905

Figure 11 shows the respective frequencies of larvae, pre-adult and adult lice per site and month. At site A nearly 80 percent of all lice were larvae whereas the two other sites have larvae frequencies of under 10 percent with site C not having any at all (**Figure 11**). All three sites have an increased amount of adult lice in August when

compared to July, with different amounts of increase (**Figure 11**). Site A has the highest amount of adult lice in August, with over 80 percent whereas Site B and C have frequencies between 60 and 70 percent (**Figure 11**).

The proportion of developmental stages per site and month are shown more detailed in Figure 12 and 13 with the former showing data for L. salmonis and the latter showing the data for *C. elongatus*. The larval stage that is dominant at site A in July is chalimus 2 with over 1 lice of this stage per sampled fish. The two dominant stages at Site B in July are pre-adult 2 female and adult male with a mean abundance of over 1 louse per fish. Adult male L. salmonis have the same mean abundance for Site C in July but there are less pre-adult 2 female lice and this site also has the highest amount of adult females per fish in July with over 0.5. Adult male and female are the two dominant stages at all sites in August, with the latter having mean abundances of over 2 lice per fish. Next highest mean numbers in August had both pre-adult 1 and 2 female with around 0.25 at site A and around 0.5 at Site B and C. The other louse species, C. elongatus, showed lower mean number in general with no developmental stage reaching a mean number of 1 louse per fish. At both Site A and B only chalimus 3 and 4 as well as adult male lice were recorded with the latter having the highest mean number at 0.3 and 0.2 respectively. Fish at Site C were carrying chalimus 4 and both adult male and female C. elongatus. Highest mean number here was 0.2 for adult female lice. The dominant stage at all sites in August was adult female with a mean number of 0.2 for Site A, 0.8 for Site B and nearly 1 for Site C. Other than that only chalimus 4 was found at Site A and adult male at Site B and C.

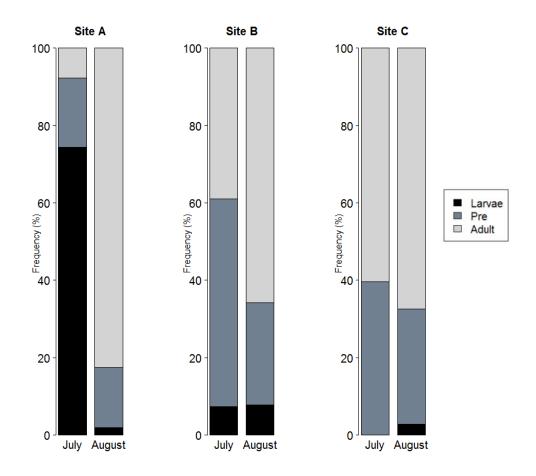


Figure 11: Frequencies of larvae, pre-adult and adult lice shown in percent of the total sea lice population, where 0 percent means that no lice of this stage were observed and 100 percent means that only lice of this stage were observed. Data is visualised separately for each sampling site and the two sampling months.

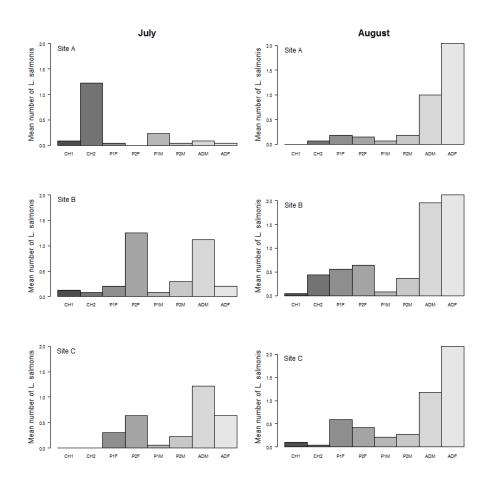


Figure 12: Mean numbers of Lepeophtheirus salmonis shown as abundances in mean numbers/fish sampled, , including the non-infected ones. Data is visualised separately for all three sampling sites and both sampling Month. Abbreviations: CH1=Chalimus 1; CH2=Chalimus 2; P1F=Pre-Adult 1 female; P2F=Pre-Adult 2 female; P1M=Pre-Adult 1 male; P2M=Pre-Adult 2 male; ADM=Adult male; ADF=Adult female

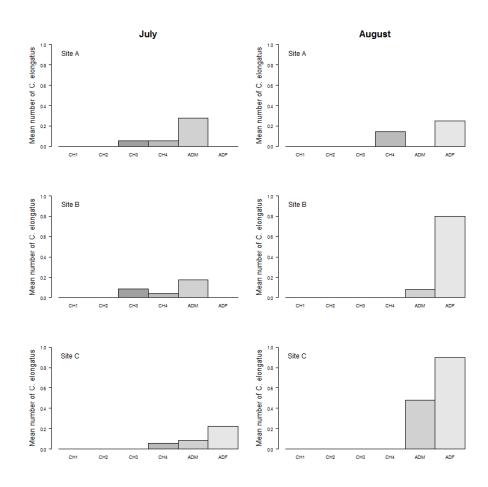


Figure 13: Mean numbers of Caligus elongatus shown as abundances, which means for all sampled fish, including the non-infected ones. Data is visualised separately for all three sampling sites and both sampling Month. Abbreviations: CH1=Chalimus 1; CH2=Chalimus 2; P1F=Pre-Adult 1 female; P2F=Pre-Adult 2 female; P1M=Pre-Adult 1 male; P2M=Pre-Adult 2 male; ADM=Adult male; ADF=Adult female

A first general Kruskal-Wallis test was done, comparing sea lice numbers for all fish between the two sampling month and it resulted in p-values of 0.29 for July and 0.09 for August. When fish of the two different size classes were analyzed, the Kruskal- Wallis test for July showed p-values of 0.48 and 0.89 for the smaller and bigger fish respectively and the test for August showed p-values of 0.22 and 0.43. As the threshold for significance was set to a value of p < 0.05, these values represent a non-significant result, meaning that the null-hypothesis, which expects no differences between the tested variable, being lice numbers per fish, has to be accepted. Results of a more detailed analysis of the two sampling month are given in **Table 7**, showing the p-values for comparisons between the three sampling sites fot both month. While the general test

delivered no significant results for neither of the two months, it can be seen in Table 7 that there actually is a slight significance in lice loads when sites A and B are compared. This significance is only slight as the p-value is lower then 0.05 but not lower then 0.01 which would be the next higher level of significance. When only considering L. salmonis there were also no significant results between the different sites per month. Pvalues were 0.09 for July and 0.06 for August. Like above, the null-hypothesis has to be accepted, meaning that there are no differences between the sites. A similar analysis was performed for C. elongatus and while the value for July was not significant, at 0.88, the value of 0.04 for August showed a slightly significant difference for infection with C. elongatus between the three different sampling sites. In the latter case the nullhypothesis is challenged, meaning that there is a difference between the three sites in the month August. The result of the Wilcoxon-Test also revealed a slightly significant difference for infection on smaller and bigger fish in the month of July with a p-value of 0.04. This challenges the null-hypothesis, meaning that there is a difference for infection rates between fish sizes. For August there was no significance detected anymore with the p-value being 0.77 and thus the null-hypothesis was accepted.

Table 7: P-values from Kruskal-Wallis tests, comparing the lice loads between the three different sampling sites for each of the two sampling month respectively. ns = not significant; * = slightly significant

	Site Comparison	p-Value	Significance
July			
	A - B	0.136	ns
	A - C	0.57	ns
	B - C	0.249	ns
August			
	A - B	0.037	*
	A - C	0.116	ns
	B - C	0.553	ns

Both salinity and temperature did not vary much between the three sites at the date of measurement. Lowest recorded value for salinity was 33.9 ‰ at a depth of ten centimetres in Fossfjördur and the highest value was 34.2 ‰ at a depth of one meter at Hjalli (**Table 8**). Temperature increased at all sites from a depth of ten centimetres to a depth of a meter. While it stagnated at all other depth at Hjalli it increased slightly in Fossfjördur and Trostansfjördur until a depth of three metres (**Table 8**). Temperature ranged from 7.6 to 8.2 degrees Celsius in Fossfjördur, from 7.8 to 7.9 degrees Celsius at Hjalli and from 7.4 to 8.2 degrees Celsius in Trostansfjördur (**Table 8**). The latter was the only site where the temperature decreased again at a depth of five metres with a decrease of 0.1 degrees Celsius (**Table 8**).

Table 8: Data for salinity in per mill (%) and temperature in degrees Celsius sampled on the 24th of October 2014 at the three sampling locations at 6 depth between 0.1 and 5 metres with specification of the exact GPS-Coordinates and place names.

Site	Name	Latitude N	Longitude W	Depth [m]	Salinity [‰]	Temp [°C]
Α	Fossfjordur	65°36'94	23°33'39	0.1	34.0	7.6
Α				1	34.0	7.9
Α				2	34.1	8.1
Α				3	34.1	8.2
Α				4	34.1	8.2
Α				5	34.1	8.2
В	Hjalli	65°39'06	23°32'49	0.1	34.1	7.8
В				1	34.2	7.9
В				2	34.1	7.9
В				3	34.1	7.9
В				4	34.1	7.9
В				5	34.1	7.9
С	Trostansfjordur	65°37'63	23°34'87	0.1	33.9	7.4
С				1	34.1	7.9
С				2	34.1	8.1
С				3	34.1	8.2
С				4	34.1	8.2
С				5	34.1	8.1

5 Discussion

While research on infection rates of sea lice on wild salmonids is a standard procedure in countries like Norway or Scotland, it has to the best of my knowledge not been conducted in Iceland before. Studies have shown that sea lice can not only have a direct lethal effect on the host fish, but that there are also various sub lethal effects. It is quite difficult to calculate or even estimate a threshold for lice abundance on the host fish at which pathogenic effects set in. Multiple studies however use a level of 0.1 lice per gram bodyweight of the host as a value for this threshold (Fast, Ross, Muise, & Johnson, 2006; Finstad & Bjørn, 2011). The wild salmonids which were sampled in this study had lice abundances which were mainly below this critical level of 0.1. In total there were nine fish, representing a percentage of 5.6 of the total sample, which exceeded this value and thus possibly being negatively impacted by the attached lice. All of these were trout, three were caught in July and six in August. The border between sub lethal and lethal effects is also very hard to determine as it will vary substantially with changes in multiple factors like stress level of the fish prior to infection or life cycle stage of the attached lice. According to Serra-Llinares et al. (2014) a level of 0.3 lice per gram bodyweight is a conservative assumption of a lethal infection threshold, at least for salmon smolts. Even if mortality of lice which are attached to a fish is considered to be non-existent, as it is described in the named study, no fish that was sampled reached this level with the highest level that was reached being 0.2 lice per gram bodyweight. It can be concluded from these facts that there is currently no acute concern for the wild salmonid stocks in the sampled areas. This conclusion however, can only be linked to one single kind of salmonid directly, which is the sea trout. As they comprise 97 percent of all caught fish and with a total of only five other salmonids this has to be the only species that is directly connected to any results. Nonetheless, scientifically valid assumptions can be made for at least salmon by using existing comparison studies of these two species in regard to louse infection (e.g. Dawson, 1997). Just recently Taranger et al. (2014) compared infestations of wild salmonids at 109 stations along the Norwegian coastline and states that wild sea trout are used as a proxy for the infection pressure on all wild salmonids in one area. This comparison

revealed that substantially more stations showed moderate to high mortality for sea trout, a total of 67 stations, than they did for salmon where only 27 stations reached those levels. While this trend indicates that trout suffer from higher infection rates than salmon it has to be considered that Icelandic stocks of those two species are different from those found in Norwegian waters and this trend might be weaker here or not evident at all. In their review of sea lice effects on sea trout Thorstad et al. (2014) summarize that the body shape of salmon and trout is different and that the body surface area is bigger for a trout than for a similar sized salmon. In regard to sea lice infection this means that trout are likely to have higher absolute numbers of sea lice than salmon. This is however, combined with the fact that the fin area of salmon is the larger of the two which could influence the settlement of lice as fins are reported to be a main site of first attachment. When these findings are combined with the results found in the present study a certain knowledge base is created for assuming that the levels of sea lice on salmon in the sampled area will be lower than the documented levels on sea trout.

Icelandic waters, especially in the northern part of the country which experiences harsher weather conditions as the southern part, are colder than those in for example Scotland and southern Norway. This leads to differences in the development time of sea lice as it is temperature dependent. Measurements from the aquaculture cages in Arnarfjörður owned by Fjarðalax (Appendix 1) show that temperatures only start ascending over three degrees Celsius in late May, eventually reaching the optimal temperature for lice development of ten degrees Celsius in late July. The period from December to May can thus be estimated to cause a very slow development of sea lice but most lice which are attached to a host will survive and infectious stages can still develop. Contradicting older assumptions that salmonids would not spend any time in salt water during the winter months it has been shown that especially in northern climates this can happen. Fish have been shown to either undertake migration to sea or even spend the whole winter at sea (Jensen & Rikardsen, 2012). The latter was mainly the case for juvenile fish that had not reached adulthood yet. As shown in the present study the overall lice load on fish with a body size of under 25 cm was significantly higher than the one for bigger fish. This could be explained by smaller fish spending the month previous to the beginning of data sampling in marine waters and thus being exposed to lice. Bigger fish are more likely to already have matured and thus returning from spawning in freshwater in which they would have lost all lice previously attached to them. Tagging studies, like done in other countries with wild salmonid populations (e.g. Davidsen et al., 2009), have delivered results which were quite frequently used in sea lice related studies, something which would also be very helpful in Iceland. Determining the actual age of caught fish will be of help for further studies as it can give further insight into postulated reasons for the higher infection of smaller fish in July. Data for temperature and salinity should also always be included in any study of this kind as changes of those factors can have substantial influence on the outcome of the study. Earlier onset of parasite reproduction which is linked to an earlier rise in water temperatures than normal, can effect the weight gain of host fish and lead to lower survival rates of salmonid smolts (Mennerat et al., 2012).

The fastest rate of lice development for the sampled area can be estimated for late July to mid-August as this is the time where sea temperatures peak. This is in accordance to the observed distribution of life cycle stages in both L. salmonis and C. elongatus as the amount of adult lice is considerably higher in August than it is in July. High infection pressures on wild salmonids can thus be expected for the period after this peak in adult lice abundance. Most of the reported epizootics in Norway also occur in this time of the year adding credibility to the results of this study. Ideally the temperature and salinity should have been measured at the three sampling locations at least once every month but this was not possible due to limitations in the accessibility of the necessary gear. The reading from the 24th of October however, is still useful as it shows that surface temperatures are still quite high at that point in time. Salmonids that stay in marine waters, up to or even after this point, are likely to show even higher intensities of lice than those sampled in August. In order to predict this we assume that adult females which were ovigerous at the point of sampling will release their eggs at the day of sampling and thus initiating the life cycle. As temperatures at that point are still around ten degrees it will take the freshly hatched lice around 40 to 60 days to reach adulthood (Pike & Wadsworth, 2000). This is a rough estimate as the exact temperatures in the

fjord system of Arnarfjörður are not known. However, even with this rough estimate it can be said that there should be a second cohort of lice which reproduces in the same salmonid migration cycle as the one sampled in August. Lice counts from fish inside the already existing net pen aquaculture support this assumption as the number of lice that are found increases throughout the month August to October (Table 2 & 3). If only the wild population of salmonids is considered, this will most likely be counteracted by the fact that most fish have either already entered freshwater or will do so soon, with only some expected to stay in the ocean. While the former kind of fish escape this proposed second wave of infectious lice in the water column entirely, the latter kind will not be influenced even by high infection rates as those lice will be shed in freshwater before they can develop into the harmful stages. The mentioned possibility of conducting a tagging study would also be interesting here, as it could estimate a ratio between fish staying in saltwater and fish entering freshwater for the winter period. If however, not only the wild salmonids but also the population of farmed salmonids is considered, things are likely to change. With an increased host population, lice that develop into the infectious stage after spawning in the proposed second wave are more likely to find attachment and subsequently survive. For the comparably small amount of aquaculture done in Arnarfjörður at the current point in time this might not be too big of an impact on the overall lice population but it is definitely something to keep in mind for future expansion plans.

The high prevalence which was found during this study could initially be seen as a cause of concern, but when compared to similar studies from other countries it becomes clear that it is not necessary as prevalence of lice on wild salmonids has generally been shown to be high. Todd et al. (2000) sampled salmon along the coastline of Ireland using bag net and reported an infestation prevalence of 100 percent while Jacobsen & Gaard (1997) used longlines in offshore areas of the eastern North Atlantic which returned a prevalence of 99.2 percent. Due to the natural presence of sea lice a certain level of infection will occur on wild salmonids which explains the found prevalence, abundances and intensities. The values for the latter are also in accordance to reports from areas without any aquaculture activity in Norway (Rikardsen, 2004). This leads

towards the assumption that the farming which is carried out in Arnarfjörður has not had a measurable influence on lice intensities on wild populations yet. As this study tested two areas close to the farms and one area which was further away and the various statistical test did not return any significant differences between these areas, only within the two proposedly exposed areas, this assumption is further verified. The lice counts which were carried by Fjarðalax on salmon in their own cages can be compared to numbers which are available for similar counts done in Norway. The abundance determined by Fjarðalax is, at a maximum, approximately three orders of magnitude lower than common abundance on salmon in Norwegian farms. Majorily these counts found no or barely any lice (Table 2). Lice counts also exist for the other existing salmon farm in Arnarfjörður, owned by Arnarlax. These show a similar trend (**Table 3**). Both, the results from this study and comparisons with other studies and countries, show that the present situation regarding sea lice on wild salmonids in Arnarfjörður is good and that there is no reason for acute concern or need for immediate actions. Nonetheless, these results do not eliminate the possibility of sea lice becoming a threat to wild salmonids just like they have in Norway or Scotland. It has to be considered that this is a pilot study and it is not known if the results are generally valid or if the situation in previous years was significantly different. To continue the effort of studying wild salmonids is of high importance. Firstly, for the already sampled area as it will show yearly trends, either validating the present conclusions or altering them either positively or negatively. Secondly, for other areas, as it has been shown that infection pressures can differ between sampling location even in the same country due to varying environmental factors. This will show if the currently non-existent threat to wild salmonids occurs just in Arnarfjörður, just in the Westfjords or for example in the whole country.

Continuing the research should be of particular interest for two parties, namely being the aquaculture industry and the freshwater fisheries. The former will want to keep the number of lice on the farmed fish as low as possible to prevent negative implications for the fish and having to apply delousing treatment. This does not directly involve the wild populations but these become of importance for expanding the salmon farming industry.

Getting licenses for new farm locations or for increasing the amount of fish in already existing farms involves various official governing bodies (as reviewed in Jonsson, 2000). These might not be willing to issue new licenses if threats to wild salmonid populations exist. Reasoning behind this assumption is the fact that wilds salmonids are of economic importance to Iceland as already pointed out. While severe epizootics similar to those in Norway or Scotland which would lead to a significant decline in wild salmonid populations are as of now unlikely there are more subtle effects which are possibly impacting the freshwater fisheries of salmonids. One impact that has been shown in recent studies is altered migratory behaviour of infected salmonids which can lead to a delayed return to freshwater (Vollset, Barlaup, Skoglund, Normann, & Skilbrei, 2014) or a decreased growth rate (Gjelland et al., 2014), both of which are negative for the purposes of freshwater angling. As shown by Agnarsson et al. (2008) the prices for freshwater angling are quite high in Iceland when compared to for instance Scotland. The scenic value of Iceland is a factor which can justify these higher prices but the quality of fish will most likely also play a role for tourists deciding to come to Iceland in order to go angling in the rivers. If numbers of angling tourists will decline with decreasing fish quality due to sea lice epizootics, is uncertain but should definitely be a reason for the freshwater angling industry to put effort into research regarding sea lice. A simple measure like counting sea lice on fish that are caught, even if they are released again can prove helpful as it creates a countrywide database which can reflect changes in general sea lice abundances.

It has already been advised that the research of sea lice infections on wild salmonids in Iceland should continue but there are some aspects to this research which became evident during the data collection and literature review for the present study that can be considered for the future. The limitation of gill-netting as a method of monitoring lice infection on wild fish have been quite well documented (reviewed in Thorstad et al., 2014) and to avoid possible short comings other methods should be considered at least in combination with gill-netting. One which stands out, because it has already been effectively used by other researchers, is the use of bag nets as a mean to catch fish. The advantages have already been named in the literature review and a detailed explanation

of the method itself is given by Barlaup et al. (2013). Another method which was developed a couple of years ago is the usage of a light emitting LED-Trap which is described as noninvasive and cost-efficient (Vinebrooke, Novales Flamarique, Gulbransen, Galbraith, & Stucchi, 2009). An aspect which is specific to the present study and will have to be reconsidered for further research is the distance to the control site. Due to certain limitations, the control site used in this study was closer to the exposed sites than it is the case in comparable studies from Norway. Bjørn and Finstad (2001) for example use a completely different fjord as control or unexposed site, which is over 100 kilometres away from the exposed site. Testing another fjord in Iceland which is similarly far away from the next marine based salmonid aquaculture will most likely result in further clarity about the effects that salmonid farms might have already had on wild populations. Additionally, the division of caught fish in size classes can be very useful as seen in other studies (Bjørn & Finstad, 2002), but how this division is done needs to be carefully considered. With most of the fish that were caught in this study being smaller then the chosen 25 cm, future studies should consider adjusting the size and maybe lower it to have a more representative division of the sample. Recent studies suggest that a risk assessment for wild salmonid stocks, which is based solely on lice caught on wild fish, is not sufficient enough due to factors like the high natural variation in infections with sea lice between individual fish (Taranger et al., 2014). In order to execute the best possible risk assessment several suggestions have been made as there does not seem to be one clearly defined most effective way. These suggestions are mainly focussed around the usage of hydrodynamic modelling of sea lice dispersal in a fjord system (Karbowski, 2015) which should be as fine scaled as possible. These models could then be backed up by the using current methods like gill- or bag-netting which could as a result of the modelling be adapted to areas where high risks are expected. A connection to an estimation of threshold levels as explained by Frazer et al. (2012) is also considered helpful as it allows for the determination of a risk level for the respective area. While it would be ideal to implement these suggested methods in Iceland as well, it has to be considered that they are substantially more expensive than simple gill-netting and also require significantly more background data. It can be concluded that an immediate movement toward these methods in Iceland is not likely

but with an expected increase in the amount of salmonid aquaculture they might be needed in the future as they will raise the chance of preventing a sea lice epizootic. There is another additional option however, which at least allows for a country-wide standardized risk assessment and has already been used in Norway. This risk assessment is explained by Taranger et al. (2014) and is based on a so called salmon lice risk index and a risk scoring system as introduced by Taranger, Svåsand, Kvamme, Kristiansen and Boxaspen (2012). In order to perform this assessment there should be a pool of data from fish catches over multiple years which is a general need for most risk assessments, confirming the need for continued research in Iceland.

6 Conclusion

In conclusion this study delivers, to the best of my knowledge, a first insight into sea lice infections on wild salmonids in Iceland and after comparing the results to studies from other countries there is no immediate call for concern. While the prevalence of lice is high, abundances and intensities are low with values below the estimated thresholds for negative impacts of lice on their hosts. As there are plans to expand the existing salmonid aquaculture, it is advised to continue the research and extend it to other susceptible areas while also implementing more distant control areas. Other methods should be considered for the future as the gill-netting has shown certain discrepancies, however it is still well suited for further collection of infection levels in a preaquaculture state.

References

- Aarestrup, K., Baktoft, H., Koed, A., del Villar-Guerra, D., & Thorstad, E. B. (2014). Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts. *Marine Ecology Progress Series*, 496, 197–206. doi:10.3354/meps10614
- Aasetre, J., & Vik, J. (2013). Framing the environment Disputes and developments in the management of Norwegian salmon fjords. *Ocean & Coastal Management*, 71, 203–212. doi:10.1016/j.ocecoaman.2012.09.001
- Agnarsson, S. (2005). Efnahagsleg áhrif lax- og silungsveiði og staða auðlindarinnar [Economic Impact of salmon and trout fishing and the status of salmonid resources]. Fræðaþing landbúnaðarins 2005
- Agnarsson, S., Radford, A., & Riddington, G. (2008). Economic impact of angling in Scotland and Iceland. *Global challenges in recreational fisheries*, 188–201.
- Asplin, L., Johnsen, I. A., Sandvik, A. D., Albretsen, J., Sundfjord, V., Aure, J., & Boxaspen, K. (2013). Dispersion of salmon lice in the Hardangerfjord. *Marine Biology Research*, 10(3), 216–225. doi:10.1080/17451000.2013.810755
- Bailey, R. J. E., Birkett, M. A., Ingvarsdóttir, A., Mordue, A. J., Mordue, W., O'Shea, B., . . . Wadhams, L. J. (2006). The role of semiochemicals in host location and non-host avoidance by salmon louse (*Lepeophtheirus salmonis*) copepodids. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(2), 448–456. doi:10.1139/f05-231
- Barlaup, B. T., Gabrielsen, S. E., Løyland, J., Schläppy, M. L., Wiers, T., Vollset, K. W., & Pulg, U. (2013). Trap design for catching fish unharmed and the implications for estimates of sea lice (*Lepeophtheirus salmonis*) on anadromous brown trout (*Salmo trutta*). *Fisheries Research*, 139, 43–46. doi:10.1016/j.fishres.2012.01.024
- Behnke, R. J. (1986). Brown trout. Trout, 27, 42-47.
- Berg, O. K., & Berg, M. (1989). The duration of sea and freshwater residence of the sea trout, *Salmo trutta*, from the Vardnes River in northern Norway. *Environmental Biology of Fishes*, 24(1), 23–32. doi:10.1007/BF00001607
- Berg, O. K., & Jonsson, B. (1990). Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardnes River, northern Norway. *Environmental Biology of Fishes*, 29(2), 145–154. doi:10.1007/BF00005031
- Bergh, O. (2007). The dual myths of the healthy wild fish and the unhealthy farmed fish. *Diseases of aquatic organisms*, 75(2), 159–164. doi:10.3354/dao075159
- Berland, B. & Margolis, L. (1983). The early history of 'Lakselus' and some nomenclatural questions relating to copepod parasites of salmon. *Sarsia*, 68(4), 281–288.
- Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (Lepeophtheirus salmonis Krøyer): migration, growth, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(12), 2808–2813. doi:10.1139/f96-231
- Bjørn, P. A., & Finstad, B. (2002). Salmon lice, *Lepeophtheirus salmonis* (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (*L.*), and sea trout, *Salmo trutta* (*L.*), in areas near and distant from salmon farms. *ICES Journal of Marine Science*, 59(1), 131–139. doi:10.1006/jmsc.2001.1143
- Bjørn, P. A., Finstad, B., & Kristoffersen, R. (2001). Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research*, *32*(12), 947–962. doi:10.1046/j.1365-2109.2001.00627.x
- Bjørn, P. A., Finstad, B., Kristoffersen, R., McKinley, R. S., & Rikardsen, A. H. (2006). Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Kroyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords. *ICES Journal of Marine Science*, 64(2), 386–393. doi:10.1093/icesjms/fsl029
- Bjørn, P. A., Finstad, B., Nilsen, R., Uglem, I., Asplin, L., Skaala, Ø. & Hvidsten, N. A., (2010). Nasjonal lakselusovervåkning 2009 på ville bestander av laks, sjøørret og sjørøye langs Norskekysten samt I forbindelse med evaluering av nasjonale laksevassdrag og laksefjorder (Norwegian national surveillance of salmon lice epidemics on wild Atlantic salmon, sea trout and Arctic charr in connection with Norwegian national salmon rivers and fjords) NINA Rapport 547. 50s.
- Bjørn, P. A., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R. M., & Kristoffersen, R. (2011). Area protection may reduce salmon louse infection risk to wild salmonids. *Aquaculture Environment Interactions*, 1(3), 233–244. doi:10.3354/aei00023

- Boxaspen, K. (2006). A review of the biology and genetics of sea lice. *ICES Journal of Marine Science*, 63(7), 1304–1316. doi:10.1016/j.icesjms.2006.04.017
- Boxaspen, K., & Næss, T. (2000). Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. *Contributions to Zoology*, 69(1/2), 51–56.
- Brandal, P. O., Egidius, E., & Romslo, I. (1976). Host Blood-Major Food Component for Parasitic Copepod *Lepeophtheirus-Salmonis* Kroyeri, 1838 (Crustacea-Caligidae). *Norwegian Journal of Zoology*, 24(4), 341–343.
- Bricknell, I. R., Dalesman, S. J., O'Shea, B., Pert, C. C., & Mordue Luntz, A. J. (2006). Effect of environmental salinity on sea lice Lepeophtheirus salmonis settlement success. *Diseases of Aquatic Organisms*, 71, 201–212. doi:10.3354/dao071201
- Bron, J. E., Sommerville, C., Jones, M., & Rae, G. H. (1991). The settlement and attachment of early stages of the salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae) on the salmon host, *Salmo salar. Journal of Zoology*, 224(2), 201–212. doi:10.1111/j.1469-7998.1991.tb04799.x
- Burridge, L., Weis, J. S., Cabello, F., Pizarro, J., & Bostick, K. (2008). Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. *Aquaculture*, 306(1-4), 7–23. doi:10.1016/j.aquaculture.2010.05.020
- Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of parasitology*, 575–583.
- Butler, J. R. A. (2002). Wild salmonids and sea louse infestations on the west coast of Scotland: sources of infection and implications for the management of marine salmon farms. *Pest management science*, *58*(6), 595-608; discussion 622-9. doi:10.1002/ps.490
- Butler, J. R. A., Radford, A., Riddington, G., & Laughton, R. (2009). Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: The economic impact of recreational rod fisheries. *Fisheries Research*, 96(2-3), 259–266. doi:10.1016/j.fishres.2008.12.006
- Butler, J. R. A., & Watt, J. (2003) Assessing and Managing the Impacts of Marine Salmon Farms on Wild Atlantic Salmon in Western Scotland: Identifying Priority Rivers for Conservation. In: *Salmon at the Edge* (ed D. Mills), Blackwell Science Ltd., Oxford, UK. doi: 10.1002/9780470995495.ch9
- Connors, B., Krkošek, M., & Dill, L. (2008). Sea lice escape predation on their host. *Biology Letters*, 4(5), 455–457. doi:10.1098/rsbl.2008.0276
- Copley, L., Tierney, T. D., Kane, F., Naughton, O., Kennedy, S., O'Donohoe, P., . . . McGrath, D. (2005). Sea lice, *Lepeophtheirus salmonis* and *Caligus elongatus*, levels on salmon returning to the west coast of Ireland, 2003. *Journal of the Marine Biological Association of the UK*, 85(1), 87–92. doi:10.1017/S0025315405010878h
- Costello, M. J. (1993). Review of methods to control sea lice (Caligidae: Crustacea) infestations on salmon (Salmo salar) farms. *Pathogens of wild and farmed fish: sea lice*, 219–252. Chichester, UK: Ellis Horwood
- Costello, M. J. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology*, 22(10), 475–483. doi:10.1016/j.pt.2006.08.006
- Costello, M. J. (2009a). How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B: Biological Sciences, 276*(1672), 3385–3394. doi:10.1098/rspb.2009.0771
- Costello, M. J. (2009b). The global economic cost of sea lice to the salmonid farming industry. *Journal of Fish Diseases*, 32(1), 115–118. doi:10.1111/j.1365-2761.2008.01011.x
- Costelloe, J., Costelloe, M., & Roche, N. (1995). Variation in sea lice infestation on Atlantic salmon smolts in Killary Harbour, West Coast of Ireland. *Aquaculture International*, 3(4), 379–393. doi:10.1007/BF00121626
- Costelloe, M., Costelloe, J., & Roche, N. (1996). Planktonic Dispersion of Larval Salmon-Lice, *Lepeophtheirus Salmonis*, Associated with Cultured Salmon, *Salmo Salar*, in Western Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 76(01), 141. doi:10.1017/S0025315400029064
- Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife--threats to biodiversity and human health. *Science*, 287(5452), 443–449.
- Davidsen, J. G., Plantalech Manel-la, N., Økland, F., Diserud, O. H., Thorstad, E. B., Finstad, B., . . . Rikardsen, A. H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, 73(4), 1065–1074. doi:10.1111/j.1095-8649.2008.02004.x

- Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., . . . Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *Journal of Fish Biology*, 75(7), 1700–1718. doi:10.1111/j.1095-8649.2009.02423.x
- Dawson, L. (1996). The physiological effects of salmon lice (*Lepeophtheirus salmonis*) infections on returning post-smolt sea trout (*Salmo truttaL*.) in western Ireland, 1996. *ICES Journal of Marine Science*, 55(2), 193–200. doi:10.1006/jmsc.1997.0358
- Dawson, L. (1997). Comparison of the susceptibility of sea trout (*Salmo trutta L*.) and Atlantic salmon (*Salmo salar L*.) to sea lice (*Lepeophtheirus salmonis* (Krøyer, 1837)) infections. *ICES Journal of Marine Science*, 54(6), 1129–1139. doi:10.1016/S1054-3139(97)80018-5
- Dieperink, C., Pedersen, S., & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta L.*) smolts. *Ecology of Freshwater Fish*, 10(3), 177–183. doi:10.1034/j.1600-0633.2001.100307.x
- Dobson, A. P., & May, R. M. (1987). The effects of parasites on fish populations—theoretical aspects. *International Journal for Parasitology*, 17(2), 363–370. doi:10.1016/0020-7519(87)90111-1
- Elliott, J. M. (1994). *Quantitative ecology and the brown trout. Oxford series in ecology and evolution.* Oxford, New York: Oxford University Press.
- Ellner, S., & Hairston Jr, N. G. (1994). Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *American Naturalist*, 403–417.
- Extreme Iceland. (n.d.) [Map of Iceland] Retrieved from: https://www.extremeiceland.is/images/mapoficeland.jpg
- FAO. (2010). Fishery and Aquaculture Country Profiles. Iceland (2010). Country Profile Fact Sheets. In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 1 May 2010. [Cited 13 February 2015].
- FAO. (2012). The state of world fisheries and aquaculture 2012. Rome, London: *Food and Agriculture Organization of the United Nations*; Eurospan [distributor].
- Fast, M. D., Johnson, S. C., Eddy, T. D., Pinto, D., & Ross, N. W. (2007). *Lepeophtheirus salmonis* secretory/excretory products and their effects on Atlantic salmon immune gene regulation. *Parasite Immunology*, 29(4), 179–189. doi:10.1111/j.1365-3024.2007.00932.x
- Fast, M. D., Ross, N. W., Craft, C., Locke, S., MacKinnon, S., & Johnson, S. C. (2004). *Lepeophtheirus salmonis*: characterization of prostaglandin E2 in secretory products of the salmon louse by RP-HPLC and mass spectrometry. *Experimental Parasitology*, 107(1-2), 5–13. doi:10.1016/j.exppara.2004.04.001
- Fast, M. D., Ross, N. W., Muise, D. M., & Johnson, S. C. (2006). Differential Gene Expression in Atlantic Salmon Infected with *Lepeophtheirus salmonis*. *Journal of Aquatic Animal Health*, *18*(2), 116–127. doi:10.1577/H05-043.1
- Fast, M. D., Ross, N. W., Mustafa, A., Sims, D. E., Johnson, S. C., Conboy, G. A., Burka, J. F. (2002). Susceptibility of rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar* and coho salmon *Oncorhynchus kisutch* to experimental infection with sea lice *Lepeophtheirus salmonis*. *Diseases of aquatic organisms*, 52(1), 57–68. doi:10.3354/dao052057
- Finstad, B., & Bjørn, P. A. (2011). Present status and implications of salmon lice on wild salmonids in Norwegian coastal zones. *Salmon lice: an integrated approach to understanding parasite abundance and distribution*, 279–305. Wiley-Blackwell, Oxford, UK. doi: 10.1002/9780470961568.ch9
- Finstad, B., Bjørn, P. A., & Nilsen, S. T. (1995). Survival of salmon lice, *Lepeophtheirus salmonis Krøyer*, on Arctic charr, *Salvelinus alpinus (L.)*, in fresh water. *Aquaculture Research*, *26*(10), 791–795. doi:10.1111/j.1365-2109.1995.tb00871.x
- Finstad, B., Kroglund, F., Strand, R., Stefansson, S. O., Bjørn, P. A., Rosseland, B. O., . . . Salbu, B. (2007). Salmon lice or suboptimal water quality Reasons for reduced postsmolt survival? *Aquaculture*, 273(2-3), 374–383. doi:10.1016/j.aquaculture.2007.10.019
- Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A., & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, 66(1), 86–96. doi:10.1111/j.0022-1112.2005.00581.x
- Ford, J. S., & Myers†, R. A. (2008). A Global Assessment of Salmon Aquaculture Impacts on Wild Salmonids. *PLoS Biology*, *6*(2), e33. doi:10.1371/journal.pbio.0060033
- Foreman, M., Czajko, P., Stucchi, D. J., & Guo, M. (2009). A finite volume model simulation for the Broughton Archipelago, Canada. *Ocean Modelling*, 30(1), 29–47. doi:10.1016/j.ocemod.2009.05.009

- Frazer, L. N. (2008). Sea-lice infection models for fishes. *Journal of Mathematical Biology*, 57(4), 595–611. doi:10.1007/s00285-008-0181-3
- Frazer, L. N. (2009). Sea-Cage Aquaculture, Sea Lice, and Declines of Wild Fish. *Conservation Biology*, 23(3), 599–607. doi:10.1111/j.1523-1739.2008.01128.x
- Frazer, L. N., Morton, A., & Krkošek, M. (2012). Critical thresholds in sea lice epidemics: evidence, sensitivity and subcritical estimation. *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), 1950–1958. doi:10.1098/rspb.2011.2210
- Gargan, P. G., Forde, G., Hazon, N., Russell, D., Todd, C. D., & Grant, J. W. (2012). Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(2), 343–353. doi:10.1139/f2011-155
- Gargan, P. G., Tully, O., & Poole, W. R. (2003). The relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001. In: *Salmon at the Edge* (ed D. Mills), Blackwell Science Ltd., Oxford, UK. doi: 10.1002/9780470995495.ch10
- Genna, R. L., Mordue, W., Pike, A. W., & Mordue, A. J. (2005). Light intensity, salinity, and host velocity influence presettlement intensity and distribution on hosts by copepodids of sea lice, *Lepeophtheirus salmonis*. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(12), 2675–2682. doi:10.1139/f05-163
- Gjelland, K. Ø., Serra-Llinares, R. M., Hedger, R. D., Arechavala-Lopez, P., Nilsen, R., Finstad, B., . . . Bjørn, P. A. (2014). Effects of salmon lice infection on the behaviour of sea trout in the marine phase. *Aquaculture Environment Interactions*, *5*(3), 221–233. doi:10.3354/aei00105
- Glover, K., Nilsen, F., Skaala, Ø., Taggart, J. B., & Teale, A. J. (2001). Differences in susceptibility to sea lice infection between a sea run and a freshwater resident population of brown trout. *Journal of Fish Biology*, 59(6), 1512–1519. doi:10.1006/jfbi.2001.1787
- Glover, K. A., Skaala, Ø., Nilsen, F., Olsen, R., Teale, A. J., & Taggart, J. B. (2003). Differing susceptibility of anadromous brown trout (*Salmo trutta L.*) populations to salmon louse (*Lepeophtheirus salmonis* (Krøyer, 1837)) infection. *ICES Journal of Marine Science: Journal du Conseil*, 60(5), 1139–1148.
- Gonzalez-Alanis, P., Wright, G. M., Johnson, S. C., & Burka, J. F. (2009). Frontal filament morphogenesis in the salmon louse *Lepeophtheirus salmonis*. Journal of Parasitology 2001; 87: 561-574.
- Good, T. P., Waples, R. S., & Adams, P., editors. (2005). Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66.
- Grimnes, A., & Jakobsen, P. J. (1996). The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. *Journal of Fish Biology*, 48(6), 1179–1194. doi:10.1111/j.1095-8649.1996.tb01813.x
- Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science (New York, N.Y.)*, 239(4845), 1291–1293. doi:10.1126/science.239.4845.1291
- Guðbergsson, G. (2008). Lax- og silungsveiðin 2007 [Salmon and trout fishing 2007]. VMST/08023. Reykjavík: Institute of Freshwater Fisheries.
- Guðbergsson, G. (2014). Catch statistics for Atlantic salmon Arctic charr and brown trout in Icelandic rivers and lakes. VMST/14045. Reykjavik: Institute of Freshwater Fisheries.
- Guðbergsson, G. & Antonsson, Þ. (1996). Fiskar í ám og vötnum Fræðirit fyrir almenning um íslenska ferskvatnsfiska [Fish that lives in rivers and lakes Scientific Book for Laymen on Icelandic Freshwater Fish]. Reykjavík: Landvernd.
- Guðjónsson, T. (1978). The Atlantic salmon in Iceland. J. Agric. Res. Icel., 10, 11-39.
- Hamre, L. A., Eichner, C., Caipang, C. M. A., Dalvin, S. T., Bron, J. E., Nilsen, F., . . . Krkošek, M. (2013). The Salmon Louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) Life Cycle Has Only Two Chalimus Stages. *PLoS ONE*, 8(9), e73539. doi:10.1371/journal.pone.0073539
- Hansen, L. P., Holm, M., Hoist, J. C., & Jacobsen, J. A. (2003). The Ecology of Post-Smolts of Atlantic Salmon. In: *Salmon at the Edge* (ed D. Mills), Blackwell Science Ltd., Oxford, UK. doi: 10.1002/9780470995495.ch4
- Hansen, L. P., & Lund, R. A. (1992). Resultater av forsaksfiske etter laks i ytre Nordfjord i januar 1992 (Results from testfishing after Atlantic salmon in outer Nordfjord in January 1992). NINA Oppdragsmelding, 101: 10 pp.

- Hansen, L. P., & Quinn, T. P. (1998). The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(S1), 104–118. doi:10.1139/d98-010
- Harris, G., & Milner, N. (Eds.). (2006). Sea Trout: Biology, Conservation and Management. Oxford, UK: Blackwell Publishing Ltd.
- Hayward, C. J., Andrews, M., & Nowak, B. F. (2011). Introduction: *Lepeophtheirus salmonis* -A Remarkable Success Story. In: *Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (eds S. Jones & R. Beamish), Wiley-Blackwell, Oxford, UK. doi: 10.1002/9780470961568.ch
- Heuch, P. A., Bjørn, P. A., Finstad, B., Holst, J. C., Asplin, L., & Nilsen, F. (2005). A review of the Norwegian 'National Action Plan Against Salmon Lice on Salmonids': The effect on wild salmonids. *Aquaculture*, 246(1-4), 79–92. doi:10.1016/j.aquaculture.2004.12.027
- Heuch, P. A., Doall, M. H., & Yen, J. (2006). Water flow around a fish mimic attracts a parasitic and deters a planktonic copepod. *Journal of Plankton Research*, 29(Supplement 1), i3. doi:10.1093/plankt/fbl060
- Heuch, P. A., & Karlsen, E. (1997). Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda Caligida). *Journal of Plankton Research*, 19(6), 735–747. doi:10.1093/plankt/19.6.735
- Heuch, P. A., Knutsen, J. A., Knutsen, H., & Schram, T. A. (2002). Salinity and temperature effects on sea lice overwintering on sea trout (*Salmo trutta*) in coastal areas of the Skagerrak. *Journal of the Marine Biological Association of the UK*, 82(5), 887–892. doi:10.1017/S0025315402006306
- Heuch, P. A., & Mo, T. A. (2001). A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. *Diseases of aquatic organisms*, 45(2), 145–152. doi:10.3354/dao045145
- Heuch, P. A., Nordhagen, J. R., & Schram, T. A. (2000). Egg production in the salmon louse [*Lepeophtheirus salmonis* (Kroyer)] in relation to origin and water temperature. *Aquaculture Research*, 31(11), 805–814. doi:10.1046/j.1365-2109.2000.00512.x
- Heuch, P. A., Parsons, A., & Boxaspen, K. (1995). Diel vertical migration: A possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? *Canadian Journal of Fisheries and Aquatic Sciences*, 52(4), 681–689. doi:10.1139/f95-069
- Hevrøy, E., Boxaspen, K., Oppedal, F., Taranger, G., & Holm, J. C. (2003). The effect of artificial light treatment and depth on the infestation of the sea louse Lepeophtheirus salmonis on Atlantic salmon (*Salmo salar L.*) culture. *Aquaculture*, 220(1-4), 1–14. doi:10.1016/S0044-8486(02)00189-8
- Hogans, W. E. (1995). Infection Dynamics of Sea Lice, Lepeophtheirus Salmonis (Copedoda: Caligidae) Parasitic on Atlantic Salmon (Salmo Salar) Cultured in Marine Waters of the Lower Bay of Fundy: Department of Fisheries & Oceans, Biological Station.
- Hvidsten, N. A., Heggberget, T. G., & Jensen, A. J. (1998). Sea water temperatures at Atlantic salmon smolt enterance. *Nordic Journal of Freshwater Research*, 79–86.
- Hvidsten, N. A., Jensen, A. J., Vivås, H., Bakke, Ø., & Heggberget, T. G. (1995). Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic Journal of Freshwater Research (Sweden)*
- ICES. 1997. Report of the Workshop on Interactions between Salmon Lice and Salmonids. ICES CM 1997/M: 4 Ref: F. 173 pp.
- Igboeli, O. O., Burka, J. F., & Fast, M. D. (2013). *Lepeophtheirus salmonis*: a persisting challenge for salmon aquaculture. *Animal Frontiers*, 4(1), 22–32. doi:10.2527/af.2014-0004
- Imsland, A. K., Reynolds, P., Eliassen, G., Hangstad, T. A., Foss, A., Vikingstad, E., & Elvegård, T. A. (2014). The use of lumpfish (*Cyclopterus lumpus L.*) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar L.*). *Aquaculture*, 424-425, 18–23. doi:10.1016/j.aquaculture.2013.12.033
- Ingvarsdottir, A., Birkett, M. A., Duce, I., Genna, R. L., Mordue, W., Pickett, J. A., . . . Mordue, A. J. (2002). Semiochemical strategies for sea louse control: host location cues. *Pest Management Science*, *58*(6), 537–545. doi:10.1002/ps.510

- Isaksson, A. (1979). Salmon ranching in Iceland. *Journées d'étude Aquaculture extensive et repeuplement-*Brest, 29-31 Mai 1979
- Jackson, D., Cotter, D., Newell, J., McEvoy, S., O'Donohoe, P., Kane, F., . . . Drumm, A. (2012). Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon *Salmo salar L.*, smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. *Journal of Fish Diseases*, *36*(3), 273–281. doi:10.1111/jfd.12054
- Jackson, D., Cotter, D., ÓMaoiléidigh, N., O'Donohoe, P., White, J., Kane, F., . . . Rogan, G. (2011). An evaluation of the impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon, *Salmo salar L.*, smolts. *Aquaculture*, 320(3-4), 159–163. doi:10.1016/j.aquaculture.2011.03.029
- Jackson, D., Deady, S., Leahy, Y., & Hassett, D. (1997). Variations in parasitic caligid infestations on farmed salmonids and implications for their management. *ICES Journal of Marine Science: Journal du Conseil*, 54(6), 1104–1112
- Jackson, D., Hassett, D., Deady, S., & Leahy, Y. (2000). *Lepeophtheirus salmonis* (Copepoda: Caligidae) on farmed salmon in Ireland. *Contributions to Zoology*, 69(1/2), 71–78.
- Jacobsen, J., & Gaard, E. (1997). Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar L.*). *ICES Journal of Marine Science*, 54(6), 1113–1119. doi:10.1016/S1054-3139(97)80016-1
- Jansen, P. A., Kristoffersen, A. B., Viljugrein, H., Jimenez, D., Aldrin, M., & Stien, A. (2012). Sea lice as a density-dependent constraint to salmonid farming. *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), 2330–2338. doi:10.1098/rspb.2012.0084
- Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H., Saksgård, L., & Bradford, M. (2012). Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 69(4), 711–723. doi:10.1139/f2012-005
- Jensen, J. L. A., & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology*, 81(2), 735–749. doi:10.1111/j.1095-8649.2012.03343.x
- Johnson, S. C., & Albright, L. J. (1991a). The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Canadian Journal of Zoology, 69*(4), 929–950. doi:10.1139/z91-138
- Johnson, S. C., & Albright, L. J. (1991b). Development, Growth, and Survival of *Lepeophtheirus Salmonis* (Copepoda: Caligidae) Under Laboratory Conditions. *Journal of the Marine Biological Association of the United Kingdom*, 71(02), 425. doi:10.1017/S0025315400051687
- Johnson, S. C., & Albright, L. J. (1992). Comparative susceptibility and histopathology oi the response of naive Atlantic, chinook and coho salmon to experimental infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Dis. aquat, Org.*, 141179, 1931992.
- Jones, S. R. M. (2001). The occurrence and mechanisms of innate immunity against parasites in fish. *Developmental & Comparative Immunology*, 25(8-9), 841–852. doi:10.1016/S0145-305X(01)00039-8
- Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society*, 114(2), 182–194.
- Jonsson, B., & Jonsson, N. (2011). Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories. Fish & fisheries series: Vol. 33. Dordrecht, New York: Springer.
- Jonsson, B., & L'Abee-Lund, J. H. (1993). Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology*, 43(sa), 1–16. doi:10.1111/j.1095-8649.1993.tb01175.x
- Jonsson, G. S. (2000). Licensing, monitoring and regulation of aquaculture in Iceland. *Journal of Applied Ichthyology*, 16(4-5), 172–176. doi:10.1046/j.1439-0426.2000.00264.x
- Kabata, Z. (1979). Parasitic copepoda of British fishes. [Publications] Ray Society: no. 152. London: Ray Society.
- Keeley, E. R., & Grant, J. W. A. (2001). Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(6), 1122–1132. doi:10.1139/cjfas-58-6-1122

Kent, M. L. (2000). Marine netpen farming leads to infections with some unusual parasites. *International Journal for Parasitology*, 30(3), 321–326.

Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar L.*, brown trout *Salmo trutta L.* and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12(1), 1–59. doi:10.1034/j.1600-0633.2003.00010.x

Kolstad, K., Heuch, P. A., Gjerde, B., Gjedrem, T., & Salte, R. (2005). Genetic variation in resistance of Atlantic salmon (*Salmo salar*) to the salmon louse *Lepeophtheirus salmonis*. *Aquaculture*, 247(1-4), 145–151. doi:10.1016/j.aquaculture.2005.02.009

Krkošek, M. (2010a). Sea lice and salmon in Pacific Canada: ecology and policy. Frontiers in Ecology and the Environment, 8(4), 201–209. doi:10.1890/080097

Krkošek, M. (2010b). Host density thresholds and disease control for fisheries and aquaculture. *Aquaculture Environment Interactions*, 1(1), 21–32. doi:10.3354/aei0004

Krkošek, M., Connors, B. M., Ford, H., Peacock, S., Mages, P., Ford, J. S., . . . Lewis, M. A. (2011). Fish farms, parasites, and predators: implications for salmon population dynamics. *Ecological Applications*, 21(3), 897–914. doi:10.1890/09-1861.1

Krkošek, M., Ford, J. S., Morton, A., Lele, S., Myers†, R. A., & Lewis, M. A. (2007). Declining Wild Salmon Populations in Relation to Parasites from Farm Salmon. *Science*, 318(5857), 1772–1775. doi:10.1126/science.1148744

Krkošek, M., Revie, C. W., Gargan, P. G., Skilbrei, O. T., Finstad, B. & Todd, C. D. (2013). Impacts of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proc. R. Soc. B.* 280(1750); doi.org/10.1098/rspb.2012.2359.

Karbowski, C. M. (2015) A First Assessment of Sea Lice Abundance in Arnarfjörður, Iceland. Sentinel Cage Sampling and Assessment of Hydrodynamic Modelling Feasibility. *Thesis in Preparation*

Lyse, A. A., Stefansson, S. O., & Ferno, A. (1998). Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, 52(5), 923–936. doi:10.1111/j.1095-8649.1998.tb00593.x

MacKenzie, K., Longshaw, M., Begg, G. S., & McVicar, A. H. (1998). Sea lice (Copepoda: Caligidae) on wild sea trout (Salmo truttaL.) in Scotland. ICES Journal of Marine Science, 55(2), 151–162. doi:10.1006/jmsc.1997.0362

MacKinnon, B. (1998). Host factors important in sea lice infections. *ICES Journal of Marine Science*, 55(2), 188–192. doi:10.1006/jmsc.1997.0361

Mennerat, A., Hamre, L., Ebert, D., Nilsen, F., Dávidová, M., & Skorping, A. (2012). Life history and virulence are linked in the ectoparasitic salmon louse *Lepeophtheirus salmonis*. *Journal of Evolutionary Biology*, 25(5), 856–861.

Middlemas, S. J., Fryer, R. J., Tulett, D., & Armstrong, J. D. (2013). Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. *Fisheries Management and Ecology*, 20(1), 68–74. doi:10.1111/fme.12010

Middlemas, S. J., Stewart, D. C., Mackay, S., & Armstrong, J. D. (2009). Habitat use and dispersal of post-smolt sea trout *Salmo trutta* in a Scottish sea loch system. *Journal of Fish Biology*, 74(3), 639–651. doi:10.1111/j.1095-8649.2008.02154.x

Mills, D. (Ed.). (2003). Salmon at the Edge. Oxford, UK: Blackwell Science Ltd.

Mills, D. (1989). Ecology and management of Atlantic salmon. London, New York: Chapman and Hall.

Mordue, A. J., & Birkett, M. A. (2009). A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). *Journal of Fish Diseases*, 32(1), 3–13. doi:10.1111/j.1365-2761.2008.01004.x

Murray, A. G. (2008). Using simple models to review the application and implications of different approaches used to simulate transmission of pathogens among aquatic animals. *Preventive veterinary medicine*, 88(3), 167–177. doi:10.1016/j.prevetmed.2008.09.006

Murray, A. G., & Gillibrand, P. A. (2006). Modelling salmon lice dispersal in Loch Torridon, Scotland. *Marine pollution bulletin*, 53(1-4), 128–135. doi:10.1016/j.marpolbul.2005.09.013

Mustafa, A., Conboy, G. A., Burka, J. F., Hendry, C. I., & McGladdery, S. E. (2000). Life-span and reproductive capacity of sea lice, *Lepeophtheirus salmonis*, under laboratory conditions. *Special Publication-Aquaculture Association of Canada*. (4), 113–114.

Mustafa, A., Rankaduwa, W., & Campbell, P. (2001). Estimating the cost of sea lice to salmon aquaculture in eastern Canada. *The Canadian veterinary journal. La revue vétérinaire canadienne*, 42(1), 54–56.

Nagasawa, K. (2004). Sea lice, *Lepeophtheirus salmonis* and *Caligus orientalis* (Copepoda: Caligidae), of wild and farmed fish in sea and brackish waters of Japan and adjacent regions: a review. *Zoological Studies*, 43(2), 173–178.

Nolan, D. T., Reilly, P., & Bonga Wendelaar, S. E. (1999). Infection with low numbers of the sea louse *Lepeophtheirus salmonis* induces stress-related effects in postsmolt Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56(6), 947–959. doi:10.1139/f99-021

Norwegian Directorate of Fisheries. (2014a). *Atlantic salmon, Rainbow trout and Trout - Grow out production*. Retrieved from http://www.fiskeridir.no/english/statistics/norwegian-aquaculture/aquaculture-statistics/atlantic-salmon-and-rainbow-trout

Norwegian Directorate of Fisheries. (2014b). *Percentage of sale for the 10 largest*. Retrieved from http://www.fiskeridir.no/english/statistics/norwegian-aquaculture/aquaculture-statistics/atlantic-salmon-and-rainbow-trout

OECD (2013). OECD Review of Fisheries: Country Statistics 2013. Paris: OECD Publishing.

Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B., & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of Freshwater Fish*, *15*(4), 446–452. doi:10.1111/j.1600-0633.2006.00176.x

Paisley, L. G., Ariel, E., Lyngstad, T., Jónsson, G., Vennerström, P., Hellström, A., & Østergaard, P. (2010). An Overview of Aquaculture in the Nordic Countries. *Journal of the World Aquaculture Society, 41*(1), 1–17. doi:10.1111/j.1749-7345.2009.00309.x

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55(S1), 281–287. doi:10.1139/d98-012

Pemberton, R. (1976). Sea trout in North Argyll Sea lochs, population, distribution and movements. *Journal of Fish Biology*, 9(2), 157–179. doi:10.1111/j.1095-8649.1976.tb04670.x

Penston, M. J., & Davies, I. M. (2009). An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. *Journal of Fish Diseases*, 32(1), 75–88. doi:10.1111/j.1365-2761.2008.00986.x

Pike, A. W., & Wadsworth, S. L. (2000). Sealice on Salmonids: Their Biology and Control. In *Advances in Parasitology Advances in Parasitology Volume 44* (pp. 233–337). Elsevier.

Randall, R. G., Healey, M. C., & Dempson, J. B. (1987). Variability in length of freshwater residence of salmon, trout, and char. In Am. Fish. Soc. Symp (Vol. 1, pp. 27-41).

Revie, C., Dill, L., Finstad, B. & Todd, C. D., (2009). Sea Lice Working Group Report. - NINA Special report 39. 117 pp

Rikardsen, A. H. (2004). Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. *Journal of Fish Biology*, 65(3), 711–722. doi:10.1111/j.0022-1112.2004.00478.x

Rikardsen, A. H., Amundsen, P.-A., Bjørn, P. A., & Johansen, M. (2000). Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. *Journal of Fish Biology*, *57*(5), 1172–1188. doi:10.1111/j.1095-8649.2000.tb00479.x

Roff, D. A. (1992). The evolution of life histories: Theory and analysis. New York: Chapman & Hall.

Ross, N. W., Firth, K. J., Wang, A., Burka, J. F., & Johnson, S. C. (2000). Changes in hydrolytic enzyme activities of naïve Atlantic salmon *Salmo salar* skin mucus due to infection with the salmon louse *Lepeophtheirus salmonis* and cortisol implantation. *Diseases of aquatic organisms*, 41(1), 43–51. doi:10.3354/dao041043

Scarnecchia, D. L., Ísaksson, Á., & White, S. E. (1989). Oceanic and riverine influences on variations in yield among Icelandic stocks of Atlantic salmon. Transactions of the American fisheries Society, 118(5), 482-494.

Schaffer, W. M. (1974). Selection for Optimal Life Histories: The Effects of Age Structure. *Ecology*, 55(2), 291. doi:10.2307/1935217

Schram, T. A. (2004). Practical identification of pelagic sea lice larvae. Journal of the Marine Biological Association of the UK, 84(01), 103-110.

Scott, W. B., & Crossman, E. J. (1973 [reprinted 1979]). Freshwater fishes of Canada ([2nd reprinting with corrections]). Bulletin / Fisheries Research Board of Canada: Vol. 184. Ottawa: Fisheries Research Board of Canada.

- Serra-Llinares, R. M., Bjørn, P. A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M., & Asplin, L. (2014). Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. *Aquaculture Environment Interactions*, 5(1), 1–16. doi:10.3354/aei00090
- Siegel, D. A., Kinlan, B. P., Gaylord, B., & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, 260, 83–96. doi:10.3354/meps260083
- Sivertsgård, R., Thorstad, E. B., Økland, F., Finstad, B., Bjørn, P. A., Jepsen, N., . . . McKinley, R. S. (2007). Effects of salmon lice infection and salmon lice protection on fjord migrating Atlantic salmon and brown trout post-smolts. In P. R. Almeida, B. R. Quintella, M. J. Costa, & A. Moore (Eds.), *Developments in Hydrobiology 195*. *Developments in Fish Telemetry* (pp. 35–42). Dordrecht: Springer Netherlands.
- Skaala, Ø., Kålås, S., & Borgstrøm, R. (2014). Evidence of salmon lice-induced mortality of anadromous brown trout (*Salmo trutta*) in the Hardangerfjord, Norway. *Marine Biology Research*, 10(3), 279–288. doi:10.1080/17451000.2013.810756
- Solomon, D. J. (2006). Migration as a Life-History Strategy for the Sea Trout. In: *Sea Trout: Biology, Conservation and Management* (eds G. Harris & N. Milner), Blackwell Publishing Ltd, Oxford, UK. doi: 10.1002/9780470996027.ch15
- Stien, A., Bjørn, P. A., Heuch, P. A., & Elston, D. A. (2005). Population dynamics of salmon lice *Lepeophtheirus* salmonis on Atlantic salmon and sea trout. *Marine Ecology Progress Series*, 290, 263–275. doi:10.3354/meps290263
- Stucchi, D., Guo, M., Foreman, M. G. G., Czajko, P., Galbraith, M., Mackas, D. L., & Gillibrand, P. A. (2011). Modeling Sea Lice Production and Concentrations in the Broughton Archipelago, British Columbia. In: *Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution* (eds S. Jones & R. Beamish), Wiley-Blackwell, Oxford, UK. doi: 10.1002/9780470961568.ch4
- Sturlaugsson, J. & Thorisson, K. 1995. Postsmolts of ranched Atlantic salmon (*Salmo salar L.*) in Iceland: II. The first days of the sea migration. ICES. C.M. 1995/M:15. 17 p.
- Sturlaugsson, J. & Thorisson, K. 1997. Migratory pattern of homing Atlantic salmon (Salmo salar L.) in coastal waters W-Iceland, recorded by data storage tags. ICES. C.M.1997/CC:09. 23 p.
- Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., . . . Finstad, B. (2014). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science: Journal du Conseil*. fsu132.
- Taranger, G. L., Svåsand, T., Kvamme, B. O., Kristiansen, T. S., & Boxaspen, K. (2012). Risk assessment of Norwegian aquaculture [Risikovurdering norsk fiskeoppdrett] (In Norwegian). *Fisken og havet, særnummer*, 2–2013.
- The Icelandic Aquaculture Association. (2013). [Graph representing the aquaculture production in Iceland divided by species.] Retrieved from: http://lfh.is/documents/China23042013.pdf
- Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P. A., & McKinley, R. S. (2007). Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Hydrobiologia*, 582(1), 99–107. doi:10.1007/s10750-006-0548-7
- Thorstad, E. B., Todd, C. D., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., . . . Finstad, B., (2014). Effects of salmon lice on sea trout a literature review. NINA Report 1044, 1-162.
- Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), 500–542. doi:10.1111/j.1095-8649.2012.03370.x
- Todd, C. D., Walker, A. M., Hoyle, J. E., Northcott, S. J., Walker, A. F., & Ritchie, M. G. (2000). Infestations of wild adult Atlantic salmon (*Salmo salar L.*) by the ectoparasitic copepod sea louse *Lepeophtheirus salmonis* Krøyer: prevalence, intensity and the spatial distribution of males and females on the host fish. *Hydrobiologia*, 429(1/3), 181–196. doi:10.1023/A:1004031318505
- Todd, C. D., Whyte, B. D., MacLean, J. C., & Walker, A. M. (2006). Ectoparasitic sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestations of wild, adult, one sea-winter Atlantic salmon *Salmo salar* returning to Scotland. *Marine Ecology Progress Series*, 328, 183–193. doi:10.3354/meps328183
- Toivonen, A. L. (1997). Socio-economics of recreational fishery: Workshop, Hotel Royal Wasa, Vaasa, Finland, 12-14 May 1997: Nordic Council of Ministers. Retrieved from https://books.google.is/books?id=4AZM7b70E6QC
- Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O. T., Nilsen, F., . . . Jackson, D. (2013). Salmon lice impact on wild salmonids and salmon aquaculture. *Journal of Fish Diseases*, 36(3), 171–194. doi:10.1111/jfd.12061

Treasurer, J. W. (2005) Cleaner fish: a natural approach to the control of sea lice on farmed fish. Vet. Bull. 75, 17-29

Tucker, C. S., Sommerville, C., & Wootten, R. (2000). An Investigation into the Larval Energetics and Settlement of the Sea Louse, *Lepeophtheirus salmonis*, an Ectoparasitic Copepod of Atlantic salmon, *Salmo salar. Fish Pathology*, 35(3), 137–143. doi:10.3147/jsfp.35.137

Tucker, C. S., Sommerville, C., & Wootten, R. (2002). Does size really matter? Effects of fish surface area on the settlement and initial survival of *Lepeophtheirus salmonis*, an ectoparasite of Atlantic *salmon Salmo salar*. *Diseases of aquatic organisms*, 49(2), 145–152. doi:10.3354/dao049145

United Kingdom Hydrographic Office. (n.d.) *Tidal prediction chart for Bildudalur*. Retrieved from: http://www.ukho.gov.uk/easytide/EasyTide/ShowPrediction.aspx?PortID=0831&PredictionLength=7

Vinebrooke, R., Novales Flamarique, I., Gulbransen, C., Galbraith, M., & Stucchi, D. (2009). Monitoring and potential control of sea lice using an LED-based light trap. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(8), 1371–1382. doi:10.1139/F09-094

Vollset, K. W., Barlaup, B. T., Skoglund, H., Normann, E. S., & Skilbrei, O. T. (2014). Salmon lice increase the age of returning Atlantic salmon. *Biology Letters*, 10(1), 20130896. doi:10.1098/rsbl.2013.0896

Volterra, V. (1926). La lutte pour la vie. Paris: Gauthier.

Wagner, G. N., McKinley, R. S., Bjørn, P. A., & Finstad, B. (2003). Physiological impact of sea lice on swimming performance of Atlantic salmon. *Journal of Fish Biology*, 62(5), 1000–1009. doi:10.1046/j.1095-8649.2003.00091.x

Ward, D. M., & Hvidsten, N. A. (2011). Predation: compensation and context dependence. In: *Atlantic Salmon Ecology* (eds Ø. Aas, S. Einum, A. Klemetsen & J. Skurdal), Wiley-Blackwell, Oxford, UK. doi: 10.1002/9781444327755.ch8

Appendix 1

Table 1: Compilation of temperature readings done in Arnarfjörður, at the salmon farm owned by Fjarðalax. Readings are shown in a 10 day interval. Temperature readings are done at 7 meters depth.

Date	Temperature [°C]
15.05.14	2.3
25.05.14	3.1
04.06.14	4.2
14.06.14	5.9
24.06.14	6.6
04.07.14	7.2
14.07.14	8.7
24.07.14	9.7
03.08.14	11.4
13.08.14	11.3
23.08.14	11.6
02.09.14	10.6
12.09.14	10
22.09.14	10.2
02.10.14	10
12.10.14	8.8
22.10.14	8.4
01.11.14	7.5
11.11.14	6.2

