Network Analysis of Salmon Lice Infestations and Connectivity Between Farms: Exploring Cluster Isolation in Norwegian Salmon Farming

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Abstract

Salmon lice *(Lepeophtheirus salmonis)* are a major constraint to the sustainable growth of the Norwegian salmon farming industry. Salmon farming in open net pens leads to a proliferation and transmission of salmon lice which increases the infestation pressure on wild salmonids. Frequent delousing treatments are being performed as lice levels reaches the regulatory limit, leading to increased production related mortality and economic losses for the farmers. Lice larvae are released from salmon farms and transported by ocean currents which result in connectivity infestation networks of lice dispersal between farms. A biophysical dispersal model was in this thesis used to simulate lice dispersal between farms. The modelled lice dispersal was simulated over a four-year period, governed by ocean currents and historical production data from farms across three production zones in Norway (PZ4, PZ5 and PZ6). A network analysis was performed to analyse lice infestation networks, connectivity between farms, to calculate isolation, and explore the possibility of further isolating clusters of farms. There were spatial variations in connectivity between farms and infestation pressure. Stronger connections and higher infestation pressure were observed at farms located in the fjords compared to open coastal areas in PZ4 and PZ5. The farms partitioned into clusters within fjords and along open coastlines, where cluster size varied based on the fjord size, the number of farms, and the length of coastline covered by the farms. The clusters were highly isolated, with high internal infestations and low external infestations. Highly isolated clusters may indicate that coordinated management practises within clusters, aimed at reducing lice infestations, may be beneficial. The individual farms had in general a lower isolation than the clusters. The farm isolation was higher in the fjords than in open coastal areas. Strategic removal of external farms within the infestation networks increased the clusters´ isolations, while simultaneously decreasing the clusters´ lice infestation pressures. Isolation may be a useful term to describe the efficacy farmers can have by coordinating their management, which can be a functional preventative strategy against salmon lice in the future.

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Abbreviations

IMR   Institute of Marine Research

PZ   Production Zone

ROMS Regional Ocean Model System

R^2 R - Squared

Table of Contents

1 Introduction

1.1 - Norwegian Salmon Farming

The Atlantic salmon (*Salmo salar* L.) farming industry in Norway has grown to become one of the nation´s largest export industries by economic value (Taranger et al., 2015), currently holding a world leading position in production of salmonid fish (FAO, 2020). The production volume has increased annually since its pioneer start in the early 1970s. However, the increase in the production volume has stagnated the past decade, remaining at approximately 1.2 million tons in 2012, 1.33 million tons in 2020 and 1.5 million tons in 2021 (Sommerset et al., 2023). The stagnation is explained by the environmental concerns that have arisen; including its interaction with wildlife, genetic introgression with escaped salmon, diseases and parasites, discharge of dissolved nutrients, and accumulation of organic material in local ecosystems (Grefsrud et al., 2023). As the world population grows rapidly, there is an increased need for sustainable protein sources. In Norway, there is a strong political interest to expand the aquaculture sector. Nevertheless, further expansion is currently hindered by the industry´s lack of environmental sustainability.

For several years, infestation of Salmon lice (*Lepeophtheirus salmonis*) on wild salmonid fish, have been considered one of the key threats to sustainable salmon farming (Taranger et al., 2015). The abundance of salmon lice has increased in response to the industry´s rapid expansion (Bøhn et al., 2022). Conventional salmon farming practices in Norway are led intensively, using open net-pens that enable direct transfer of pathogens and parasites between wild and farmed fish (Sandvik et al., 2021a). Intensive production is characterized by high fish density in a confined area, leading to increased capacity for lice reproduction due to a higher availability of hosts (Dempster et al., 2021). Consequently, the infestation pressure from salmon lice is significantly higher in areas with intensive farming, compared to areas without farming (Bjørn et al., 2001). Salmon lice infestation originating from salmon farms can transmit to wild populations, affecting their survival, growth, and migration (Bjørn et al., 2001).

Industries often demonstrate their relevance and legitimacy to society by linking their practices to a sustainable development (Olsen et al., 2021). The sustainability concept has its origin from the Brundtland Report of 1987 (Brundtland, 1987), and has since evolved into a three dimensional framework, introduced by John Elkington with "the triple bottom line" (Elkington, 1997). He argued that a sustainable development is achieved by not only considering economic aspects, but also preserving environmental and social considerations. In achieving a sustainable development, it is therefore crucial to harmonize economic growth, social inclusion, and environmental protection. Salmon lice are causing high mortality rates, high treatment costs, reduced fish welfare, and economic losses for the farmers, casting the industry in an unfavourable light in the media. Salmon lice infestations thus significantly impact the sustainability in salmon farming in all three aspects.

To accomplish a predictable and sustainable growth, the importance of environmental sustainability has been emphasized as the fundamental prerequisite in regulating further expansion of the salmon farming industry (Meld. St. 16 (2014-2015)). Salmon lice and the impact on wild salmon populations are the most relevant environmental indicator in regulating regional growth. This is due to evidence suggesting a correlation between salmon biomass and salmon lice infestations (Dempster et al., 2021; Grefsrud et al., 2023). The industry may enhance its overall sustainability by addressing lice infestations, and focusing on improving the environmental sustainability.

New technology, innovations, treatment methods and digital tools are continually being developed in the combat against lice, and as we acquire knowledge regarding lice biology, behaviour and dispersal. The Norwegian salmon farming industry is ambitious, and expressing a high wish for further growth, and a strong need to solve environmental challenges. Thus, it is essential that the industry adapt a sustainable development.

1.2 - Salmon Lice Biology

The salmon louse *(Lepeophtheirus salmonis)* is a naturally occurring, marine ectoparasitic copepod infecting salmonids, such as Atlantic salmon (*Salmo Salar*), in the Northern Hemisphere. It is an obligate parasite feeding on skin, blood and mucus of its host.

1.2.1 - Development, Behaviour and Dispersal

Salmon lice display a relatively simple life cycle and require only one host for completion (Hayward et al., 2011). There are two planktonic nauplius stages that are free living, followed by an infective copepodid stage that are host searching and infectious (Hamre et al., 2013). The planktonic stages serve as the dispersal phase in the life cycle (Boxshall and Özak, 2022). The dispersal characteristics are influenced by the current speed and direction, interacting with larvae behaviour and environmental conditions (Johnsen et al., 2014). If the lice successfully find and attach to a host during the copepodid stage, they enter the chalimus stages. There are two chalimus stages during which they find a site on a host fish and emerge as attached individuals (Hamre et al., 2013). Subsequently, they transition into mobile preadults in two stages, before they ultimately molt into reproductive adults (Hamre et al., 2013; Johnson and Albright, 1991). The behaviour of lice varies within the life cycle. The preadult and adult stages are parasitic, but as mobile lice moving across the surface of the fish. When salmon lice become adults, the females produce eggs organized in two eggstrings (Pike and Wadsworth, 1999). The eggstrings are attached to the female until hatching directly into the water column as nauplii larvae. The newly hatched larvae disperse by the ocean currents as free living planktonic lice (Boxaspen, 2006).

During the planktonic stages the louse´s behaviour is controlled by the search of favourable water conditions and to settle in a position in the upper part of the water column that require lowest energy to maintain (Bui et al., 2022). Salmon lice have the ability to move vertically, but reside close to the surface as non-feeding larvae (Johnsen et al., 2016). They perform daily vertical migrations with shallower depth distributions at daytime where the chance of encounter potential hosts is highest. Host location is a critical process in the life cycle. With the goal of encounter potential hosts, the copepodids position themselves and respond to environmental cues such as salinity, light, pressure, and possibly temperature (Mordue (Luntz) and Birkett, 2009).

1.2.2 - Responses to Environmental Cues

Lepeophtheirus salmonis occurs only in cold temperature waters of the Northern Hemisphere (Hayward et al., 2011). The development is directly dependent on water temperature in all lice stages (Hamre et al., 2019; Samsing et al., 2016b). The reduction in minimum development time occur when the water temperature increases, which means there is a negative correlation

between temperature and development times (Hayward et al., 2011; Samsing et al., 2016b). In warmer waters, salmon lice thus move more quickly through the development stages making the survival time shorter (Hamre et al., 2019; Samsing et al., 2016b). Negative correlation with temperature also applies to adult body size and reproductive outputs (Hamre et al., 2019; Samsing et al., 2016b). Salmon lice develop normally through the development stages within a temperature range of 6 to 21°C (Hamre et al., 2019), which is the normal temperature range of the sea water in Norway. The louse´s development is severely constrained at 3°C (Hamre et al., 2019). The maximum temperature for normal development is between 21 and 24°C (Hamre et al., 2019).

Salmon louse larvae are phototactic, typically moving towards the light, with help of photoreceptors detecting light stimuli (Novales Flamarique et al., 2000). There are indications that copepodids can detect changes in pressure, and therefore showing depth preferences (Bron et al., 1993). The lice swim upwards in response to pressure, and changes in water flow induce bursts of swimming (Bron et al., 1993; Coates et al., 2020).

Salmon lice prefer full-salinity water with the avoidance of sites with brackish and low salinity waters (Crosbie et al., 2019). The strength of avoidance differs between the nauplii and copepodid stages. Nauplii avoid salinities below 30 ppt and have a strong clustering within the halocline (Crosbie et al., 2019). Copepodids have a more gradual proportion with declining presence of lice in layers with less saline (Crosbie et al., 2019). Copepodids prefer high salinity, and are typically present in layers with 32 and 34 ppt. However, some individuals are even found at 16-20 ppt salinity levels (Crosbie et al., 2019). The tolerance to brackish waters is thus higher in copepodids than in nauplii stages.

The attachment process of salmon lice requires sufficient contact time with the host, allowing the copepodid to attach to the fish using its clawed antennae to pierce the fish´s skin (Bron et al., 1991). Studies have shown that light, salinity, current velocity, and host behaviour, determine the distribution and number of lice settling on a host (Genna et al., 2005; Samsing et al., 2015, 2016b). Optimal infection occurs at moderate swimming speed of salmon, compared to low or high velocities (Samsing et al., 2015). Low salinity levels may reduce lice settlement (Tucker et al., 2000). Current velocity influence the attachment process, but not post-settlement

survival (Samsing et al., 2015). Copepodids attach principally on the ventral surface along the body and on the fins and dorsal fin (Bron et al., 1991).

1.2.3 - Infection of Salmon Lice on Salmonids

Salmon lice infect salmonids during their marine phase. Affected salmonids experience physical damage with open, painful wounds, due to the parasite´s attachment and feeding activity (Hayward et al., 2011). The extent of damage depends on the number of lice and become more severe when lice develop from immobile larvae to mobile lice (Grimnes and Jacobsen, 1996). The parasite is causing unnecessary suffering to the fish. Moreover, they become more susceptible to secondary infections due to the parasite´s feeding on the skin and mucous layer, thereby reducing its functioning as a protective barrier. Infection can thus lead to immunosuppression, anaemia, and chronic stress, which may further disrupt feeding patterns, reduce swimming performance, and growth (Finstad et al., 2011; Finstad and Bjørn, 2011; Wagner et al., 2003). In highly infected individuals, the fish may experience physiological challenges, osmoregulatory failure, and ultimately death (Bjørn et al., 2001; Dawson et al., 1999).

Clinical signs of infection include skin erosion, that develop to skin lesions and open wounds with time and with higher levels of infection (Bron et al., 1991). The effects on the host are related to host species, number of parasite present, and development stages of the host. As salmonids are anadromous species, the transition from freshwater to saltwater, known as the smoltification stage, is a significantly vulnerable stage to lice infestations. Mortality are typically associated with the development of lice to mobile preadult stages and adult stages (Grimnes and Jacobsen, 1996). There has been found a significant correlation between lice loads and probability of mortality under laboratory conditions (Ives et al., 2023). The level of lice that can cause 50% probability of mortality due to direct damage from lice is 0.24 lice g^{-1} (Ives et al., 2023). Other studies have suggested 100% probability of mortality at lice loads of 1.6 g^{-1} (Bui et al., 2024). The threshold vary with fish weight, and are lower for smolts than for adult fish (Ives et al., 2023).

1.3 - Environmental Impacts of Salmon Lice

The infestation pressure in farming dense regions has increased significantly over time, impacting both farmed and wild salmonids (Taranger et al., 2015). Annual lice epidemics are most likely connected to the density of salmon farms in addition to seasonal dynamics on lice infections on farmed salmon (Taranger et al., 2015). Salmon farming increases the abundance of salmon lice due to increased availability of hosts. The infection pressure around a single farm can exceed ambient levels by 70 times (Krkošek et al., 2005). The dispersal of salmon lice between farms can lead to increased lice populations, resulting in a non-sustainable infestation pressure on wild salmonids (Boxshall and Özak, 2022).

Salmon lice induced mortality on wild salmon populations are considered as one of the main concerns in the salmon farming industry. Evidence suggests that there is a connection between farm-intensive areas and the infestation of salmon lice on wild salmonids (Thorstad and Finstad, 2018). In fact, high density of lice larvae have the potential to decrease populations of wild salmonids across extensive geographical areas (Taranger et al., 2015). Wild salmonids may become more vulnerable to predation because of compromised performance and swimming speed, reducing the fish´s chances of survival (Ives et al., 2023). Atlantic salmon post-smolts are particularly vulnerable due to their small size, and effects on wild salmon stocks are particularly related to mortality on salmon smolts (Finstad et al., 2001; Grefsrud et al., 2023; Skaala et al., 2014). Moreover, research has discovered changes in population abundance, age structure and life history traits (Thorstad and Finstad, 2018). The population effects can thus be severe if sustained over time, ultimately decreasing the number of adult fish, resulting in reduced salmon stocks in the future. Conserving wild salmon stocks is thus crucial in ensuring a sustainable production and growth.

1.4 - The Norwegian Management System

Norway has a leading position of knowledge-based management of the salmon farming industry (Grefsrud et al., 2023). The farmers are required to weekly count and report the average number of adult female lice, and mobile, and attached lice based on a random sample of 20 fish (Forskrift om lakselusbekjempelse, 2012). The permitted threshold level of sea lice is 0.5 adult female lice per salmon (Forskrift om lakselusbekjempelse, 2012). To further reduce infestations on wild salmon, the threshold level in spring is lowered to 0.2, which is the time of the

outmigration of post-smolts (Forskrift om lakselusbekjempelse, 2012). Measures and treatments need to be initiated if the number of salmon lice exceeds the threshold limit, requiring routines for delousing operations and evaluations of the efficacy. Additionally, farmers must coordinate fallowing of sites at least two months after each production cycle to reduce cross-contamination (Bron et al., 1993; Huserbråten and Johnsen, 2022).

1.4.1 - The Traffic Light System

The Traffic Light System was implemented in 2017 to facilitate predictable and environmentally sustainable growth in the salmon farming industry. The intention is to ensure long-term conservation of wild salmon populations by regulating future growth. The coast of Norway is divided into 13 production zones (PZs) where the sustainability status are evaluated each year (Ådlandsvik, 2015; Produksjonsområdeforskriften, 2017). The sustainability indicator at basis for the assessment is the estimated mortality of wild salmon fish caused by salmon lice within each production zone (Meld. St. 16 (2014-2015); Vollset et al., 2021, 2022, 2023b). Estimated mortality of wild salmon is evaluated as low at <10%, providing the respective PZ a green colour, whereas a mortality between 10-30% results in a yellow colour. The estimated mortality is evaluated as high at >30% assigning the PZ a red colour. The three different traffic light colours determine whether the farms in the PZ are allowed to increase its production biomass by 6% (green), maintain its current biomass (yellow) or decrease the production biomass by 6% (red). Salmon lice induced mortality on wild salmon is currently the only indicator that regulates future growth of the industry today.

1.5 - Farm Management

Controlling infestation levels of salmon lice is troublesome and expensive, but very important. The importance lies not only in reducing production losses or to improve fish welfare, but primarily to preserve wild salmonid populations (Overton et al., 2018). An integrated strategy of several methods in combating salmon lice are required in efficient louse control (Boxshall and Özak, 2022; Sommerville, 1998). This include delousing treatments, physical prevention, selective breeding, development of vaccines, functional feeds, and the use of cleaner fish. Delousing treatments post infestation and preventative methods are most used in battling lice infestations in the farms today (Barrett et al., 2020).

1.5.1 - Delousing Treatments

Delousing treatments are separated into three categories: mechanical, chemotherapeutic, and biological; all focusing on treating the fish after infection of lice has occurred. Lice delousing using chemotherapeutants include bath treatments and in-feed additives. Non-medicinal alternatives, including biological and mechanical lice treatments, are developed technologies used as alternatives due to evolved resistance towards chemotherapeutants (Aaen et al., 2015). The use of cleaner fish that directly remove lice from the fish has been a common practice and have a continuous lice control effect (Barrett et al., 2020). Yet, there are uncertainties regarding their efficacy, and their welfare and sustainability have been of concern (Overton et al., 2020; Stien et al., 2020). Mechanical treatments include freshwater, thermal, brushing, high-pressurizes and washing methods. Mechanical and thermal delousing have proven highly effective with little impact on non-target species. However, they are stressful for the fish as the technology require crowding, pumping of fish, and temperature changes, potentially leading to elevated mortality rates and poor welfare (Overton et al., 2018). Furthermore, freshwater or low salinity baths are also used, but come with potential of developing resistant lice (Overton et al., 2018). The approaches mentioned are implemented as a reaction to existing lice infestations and are not typically effective against newly attached lice, nor are they preventative against future lice infestations (Barrett et al., 2020).

1.5.2 - Preventative Technology

Preventative methods consists of technology and approaches that aim in reducing the rate of new infestations (Barrett et al., 2020). Preventative methods can be classified in (i) technology developed to reduce encounter rates between salmon and infective copepodids, or (ii) interventions that reduce the attachment success (Barrett et al., 2020). Preventative technologies utilize louse physiology, behaviour, and swimming depth preferences along with environmental parameters to reduce infestation rates. Barrier technologies are barriers that prevent infective copepodids from entering the cage while still permitting full water exchange (Barrett et al., 2020). Skirt or snorkel barriers are examples that prevent lice from entering at the upper part of the water column (Oppedal et al., 2017). Salmon prefer to reside below the level of the barrier, protecting the fish that choose to reside in the upper surface layers, and encouraging the fish to swim at deeper depths where the infestation risk is lower (Barrett et al., 2020). The efficacy of barrier technology is related to the extent of coverage. Manipulation of swimming depth to depths where lice is least abundant is another approach in reducing encounter rates between

salmon and lice (Barrett et al., 2020). Deep swimming behaviour can be achieved by deep feeding, lighting or through submerging cages (Bui et al., 2020; Glaropoulos et al., 2019).

Functional feeds, vaccines and the breeding of more resistant salmons are preventative interventions that aim in reducing the louse´s attachment success. Functional feeds are feeds that offer physiological advantages beyond general nutritional needs (Barrett et al., 2020; Tacchi et al., 2011). Vaccines are currently still in development and have the potential to be an economically efficient solution if successfully developed in the future. There is also potential in selective breeding for lice resistance. Transfer of salmon production to fully closed, floating sea cages have also been suggested as a promising solution to mitigate salmon lice pressure (A. Nilsen et al., 2017). In closed confinement systems the infective salmon lice copepodids are avoided by pumping intake water from deeper water layers where the lice normally don´t reside (Nilsen et al., 2020).

1.6 - Spatiotemporal Management

Spatiotemporal management are additional preventative measures to reduce encounter rates and infestation risk of infective copepodids of salmon lice (Barrett et al., 2020). The infestation pressure within each farm on the coast of Norway varies significantly between locations. Some farms have low lice pressure, whereas other farms have high pressure with high risk of infestation. Lice drift with the ocean currents over long distances, creating connectivity networks between farms. Connectivity is former defined as the dispersal potential of lice between salmon farms (Samsing et al., 2017). As delousing treatments do not offer long-term protection, re-infestation from adjacent farms may occur due to connectivity (Samsing et al., 2019). Planning the spatial of farms by removing farms, fallowing farms, submerging, or closing the cages, may reduce re-infestations and dispersal of lice between farms and thus the dispersal to wild populations (Samsing et al., 2019, 2017). Locating farms to exploit beneficial oceanographic conditions, and reducing connectivity between farms may reduce encounter rates between salmon and lice (Barrett et al., 2020).

1.6.1 - Hydrodynamic Models

Understanding how salmon lice disperse and drivers of connectivity are needed in developing effective lice management strategies (Samsing et al., 2017). To address the complexity of

transmission dynamics in the ocean, different models have been used to study louse transmission (Samsing et al., 2019). Hydrodynamic models are a tool that have been widely used to study the dispersion of salmon lice, utilizing a high spatial and temporal resolution (Asplin et al., 2014; Bøhn et al., 2022; Huserbråten and Johnsen, 2022; Johnsen et al., 2016; Jones and Beamish, 2011; Murray and Gillibrand, 2006; Salama and Rabe, 2013; Samsing et al., 2019, 2017, 2016a; Sandvik et al., 2020). The Institute of Marine Research (IMR) in Norway has developed a national operational model that accurately quantifies the number of infective salmon lice through the coupling of a hydrodynamic model with a particle tracking model, creating a biological-physical dispersal model. The coupled model enables a simulation of pelagic salmon lice behaviour (Sandvik et al., 2020), and further analyses of connectivity networks and infestation patterns (Huserbråten and Johnsen, 2022; Samsing et al., 2019). The hydrodynamic models can be used to quantify lice dispersal distance, explore dispersal patterns, map areas with high salmon lice pressure, and identify connectivity between salmon farms (Huserbråten and Johnsen, 2022; Johnsen et al., 2016; Samsing et al., 2019).

Connectivity networks of salmon lice between farms are a result of oceanographic forces where lice drift with the ocean currents (Oppedal et al., 2022; Samsing et al., 2017). Seasonal variations in lice development times, oceanographic dynamics and topological arrangement of salmon farms influence the patterns of lice dispersal (Samsing et al., 2017). The infestation pressure of salmon lice intensifies during spring and summer when higher temperature accelerates their developmental cycles. The lice thus develop faster into copepodids and have a shorter lifespan, making the dispersal distance shorter (Huserbråten and Johnsen, 2022). At winter when the temperature is lower, the infestation pressure decreases. However, the lice will develop slower, and are viable for longer periods of time, thereby drifting over larger geographical areas (Huserbråten and Johnsen, 2022; Samsing et al., 2017). Lice thus can affect farms longer away, making the connectivity network more complex and extensive.

1.7 - Production Zones

Along the coast and in fjords of Norway, more than 1000 locations are approved for salmon farming production. There are 13 production zones defined based on the minimum cross-dispersion of lice between farms (Ådlandsvik, 2015). Farms within one production zone (PZ) are less likely to infest farms in another PZ. Therefore, each PZ can be seen as independent management units (Sandvik et al., 2021a). Production zone 2-7 and 10 encompass the most

production-intensive areas along the coast, featuring favourable temperature and salinity conditions for salmon lice (Grefsrud et al., 2023). The study area encompasses three production zones in Norway, each with three different traffic light colours, indicating low, moderate, and high impact on wild salmonid populations. The physical environment is a complex circulation system observing variations in currents, temperature and salinity (Samsing et al., 2017). The movement of the surface layers, where sea lice reside, is influenced by freshwater inflow from rivers, heat transfer, wind, tides, and internal waves (Asplin et al., 2014; Samsing et al., 2017).

1.8 - Aim of the Study

Previous network analyses have revealed seasonal temperature regulations of connectivity of salmon louse and identified clusters of farms where the infestation potential is higher within each cluster than between them (Huserbråten et al., 2020a; Huserbråten and Johnsen, 2022). However, less attention has been paid in exploring the degree of isolation of the clusters of farms in the infestation network. Farms can strategically be placed to minimize connectivity (Samsing et al., 2019), and there has been demonstrated that focused management may dramatically reduce densities of lice at farms (Adams et al., 2015). The purpose of this study is to examine connectivity networks of lice infestation between salmon farms in Norway, and investigate if clusters of farms can be isolated. We use a coupled biological-physical model of lice dispersal to *(i)* map the infestation network, clusters, and connectivity between farms, *(ii)* calculate the isolation ratio of individual farms and clusters of farms, and *(iii)* explore the possibility of further isolating the clusters in the network through examination of the external infestation in the connectivity network.

2 Materials and Methods

The study was performed in collaboration with the Institute of Marine Research (IMR) in Norway. A biophysical dispersal model was used to collect data of lice dispersal and to further examine network of lice infestations between farm sites (Huserbråten and Johnsen, 2022; Samsing et al., 2017).

2.1 - Description of the Study Area

The study area encompassed three production zones in Norway. The PZs selected were production zone 4 (PZ4) that represented a red area, production zone 5 (PZ5) that represented a yellow area, and production zone 6 (PZ6) that represented a green area (Figure 2.1). The traffic light colours of each production zone in the study area were assigned in 2021, based on impact of the time period of 2020-2021 (Biering et al., 2021; https://trafikklyssystemet.no). The selected PZs cover the western coast and central coast of the country, and are characterized by fjords, islands, and bays.
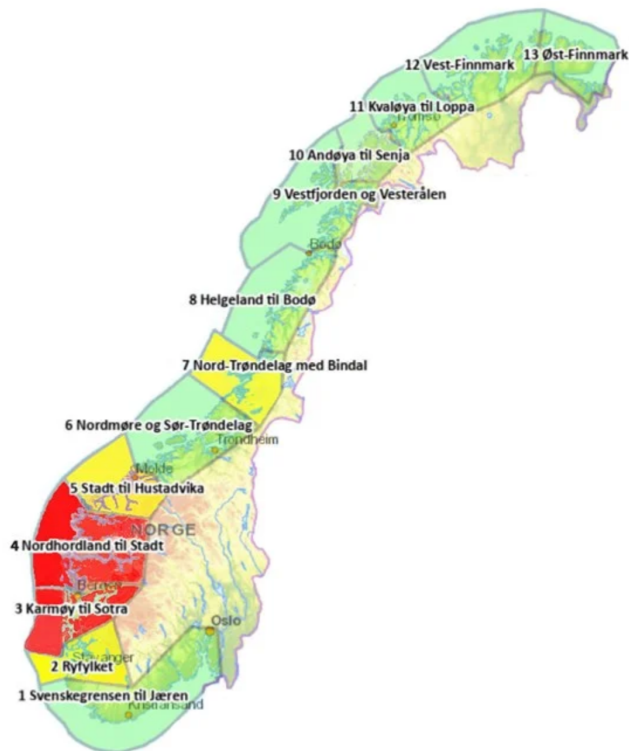
Figure 2.1: Traffic light colours of each production zone in Norway based on salmon lice impact on wild salmon in 2020-2021 (Nærings- og fiskeridepartementet, 2022).

2.1.1 - Production Zone 4

Production zone 4 covers a 30 751km^2 large area with a 6983 km^2 area of sea (Grefsrud et al., 2023). In PZ4 there were 119 salmon farms that reported fish throughout the year of 2021 (Grefsrud et al., 2023). The average monthly biomass was 81 245 tons of salmonids. The salmon farming production is conducted in fjords, in moderately exposed fjords and a smaller part in wave-exposed coast (Grefsrud et al., 2023). The average temperature in the upper part of the water column is 14-15°C during the summer and 5-6°C during the winter (Grefsrud et al., 2023). The reported mortality of farmed salmon was high in PZ4 (23-27%) in comparison to the national mortality average (15%) in 2022 (Grefsrud et al., 2023). The mortality of migrating post-smolt salmon caused by salmon lice infestation from salmon farming has been estimated as high (>30%) most years (Grefsrud et al., 2023). In 2021 the PZ was assigned a red colour.

2.1.2 - Production Zone 5

Production zone 5 covers a 14 909 km^2 large area with a 4933 km^2 area of sea (Grefsrud et al., 2023). There were 37 salmon farms that reported fish throughout the year of 2021 (Grefsrud et al., 2023). The average monthly biomass was 43 460 tons of salmonids. The farming of salmon is conducted in fjords, moderately exposed fjord areas and a minor part in wave-exposed coast. The average temperature in the upper part of the water column is normally around 14°C in the summer and 5-6°C in the winter (Grefsrud et al., 2023). The reported mortality in PZ5 has increased from below to above the national mortality average rate of 15% between 2018 to 2020 (Grefsrud et al., 2023). The mortality of migrating post-smolt salmon caused by salmon lice infestation originating from salmon farming has been estimated as moderate (10-30 % mortality), and in 2021 the PZ were assigned a yellow colour.

2.1.3 - Production Zone 6

Production zone 6 covers a 29 579 km^2 large area with a 12 371 km^2 area of sea (Grefsrud et al., 2023). There were 109 salmon farms that reported fish throughout the year of 2021 (Grefsrud et al., 2023). The average monthly biomass was 147 783 tons of salmonids. The farming of salmon is mostly conducted on wave-exposed coast, except of some farms that are located in fjords. The average temperature in the upper part of the water column is normally between 13-14°C in the summer and 6°C in the winter (Grefsrud et al., 2023). The reported mortality in PZ6 for the 2018-2020 generations was between 13-16%, which is around the national level. The mortality of migrating post-smolt salmon caused by salmon lice infestation originating from salmon farming has been estimated as low to moderate, assigning the PZ a green colour in 2021. (Grefsrud et al., 2023; Vollset et al., 2021, 2020).

2.1.4 - Description Overview

An overview of biomass, mortality and sea area measurements across the three production zones are presented in Table 2.1. The data are derived from fish generations 2020 and 2021. The ratio between biomass and sea area describes the intensity of production within each PZ. The production intensity is highest in PZ4 and PZ6, and slightly lower in PZ5. Consequently, the observed production mortality was highest in PZ4 and lowest in PZ6.

Table 2.1: Summarized description of the number of farms, biomass, mortality, sea areal and the ratio of biomass and sea area for PZ4, PZ5 and PZ6 in 2021 (Grefsrud et al., 2023; Sommerset et al., 2023).

	Farms reported fish	Biomass of salmonids	Mortality in production	Sea areal	$\dfrac{Biomass}{Sea\ area}$
PZ4	119	81 245	22.5 %	6983 km^2	11.63
PZ5	37	43 460	18.7 %	4933 km^2	8.81
PZ6	109	147 783	14.0 %	12 371 km^2	11.95

2.1.5 - Evaluations of Salmon Lice Induced Mortality

The traffic light system is designed to function as a predictable regulatory framework. In odd-numbered years, evaluations are based on the estimated impact on wild salmonid populations observed from the preceding two years. These evaluations result in regulatory consequences. Conversely, evaluations in even-numbered years provide an indication of the current impact, serving as a preliminary indicator informing the status of each production zone. In selecting of the study area, the traffic light colours given in 2021 were used as basis. These traffic lights colours were based on evaluated impact from 2020 and 2021 (Vollset et al., 2021). Our study period encompasses the years 2017 to 2021. Since the traffic light colours are based on assessments from 2020 and 2021, we ensured appropriately alignment between the salmon lice induced mortality assessments and the data from our study period.

Table 2.2: Salmon lice induced mortality on wild populations. Evaluation of traffic light colours from the expert group in the time period of 2016-2023 (F. Nilsen et al., 2017; Nilsen et al., 2018; Vollset et al., 2023, 2022, 2021, 2020, 2019).

Evaluation by expert group	2016	2017	2018	2019	2020	2021	2022	2023
PZ4	Moderate (10-30%)	High (<30%)	Moderate (10-30%)	High (<30%)	Moderate (10-30%)	High (<30%)	High (<30%)	Moderate (10-30%)
PZ5	Moderate (10-30%)	Moderate (10-30%)	Moderate (10-30%)	High (<30%)	Low (<10%)	Moderate (10-30%)	Moderate (10-30%)	Moderate (10-30%)
PZ6	Moderate (10-30%)	Low (<10%)	Low (<10%)	Low (<10%)	Low (<10%)	Low (<10%)	Moderate (10-30%)	Moderate (10-30%)

2.1.6 - Salinity, Temperature and Current Velocity

The ocean´s annually average temperature, salinity and general circulation with current velocity and direction, were plotted of the Norwegian coastline covering each PZ (Figure 2.2-2.4). The plots were made by Johnsen from the IMR to use in this study (I. Johnsen, pers. comm., June 2023). The salinity levels are highest in open sea and exposed coastal areas, with a gradual decrease in salinity moving towards the coast and inward the fjords (Figure 2.2). This applies to the entire coast and is consistent across all three PZs. The water temperature decreases moving from south to north along the Norwegian coastline (Figure 2.3). The highest temperature is observed in PZ4, showing a gradient that decreases closer to the coast, and inward the fjords. However, some southern located fjords show higher temperature in their inner parts. The temperature is lower in PZ5 and PZ6, but with a slightly warmer temperature in the southern fjords of PZ5. The temperature northwards remains consistently low. The lower salinity and temperature water in the fjords are explained by freshwater influence by rivers. The longer the fjord, the lower salinity is observed. The water current flows in a northern direction along the entire coast, with the highest average current velocity in the open sea, and the southern regions of PZ4 (Figure 2.4). The current velocity increases at the boundary between fjord mouths and the open sea and remain relatively high in the centre of the fjords.
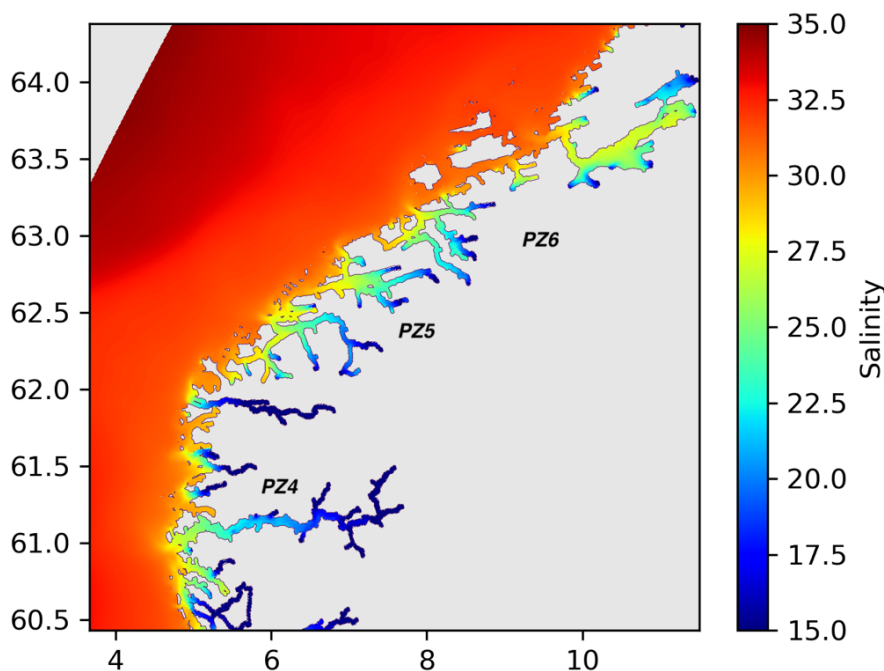

Figure 2.2: Salinity levels of the surface water of the Norwegian coast covering PZ4, PZ5 and PZ6.
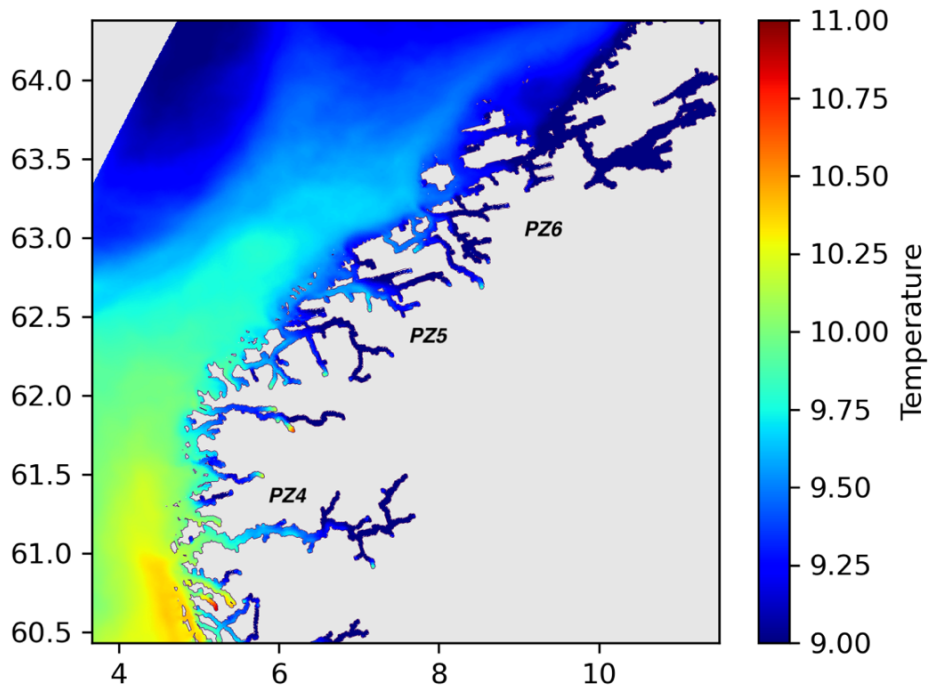
Figure 2.3: Temperature of the surface water of the Norwegian coast covering PZ4, PZ5 and PZ6.
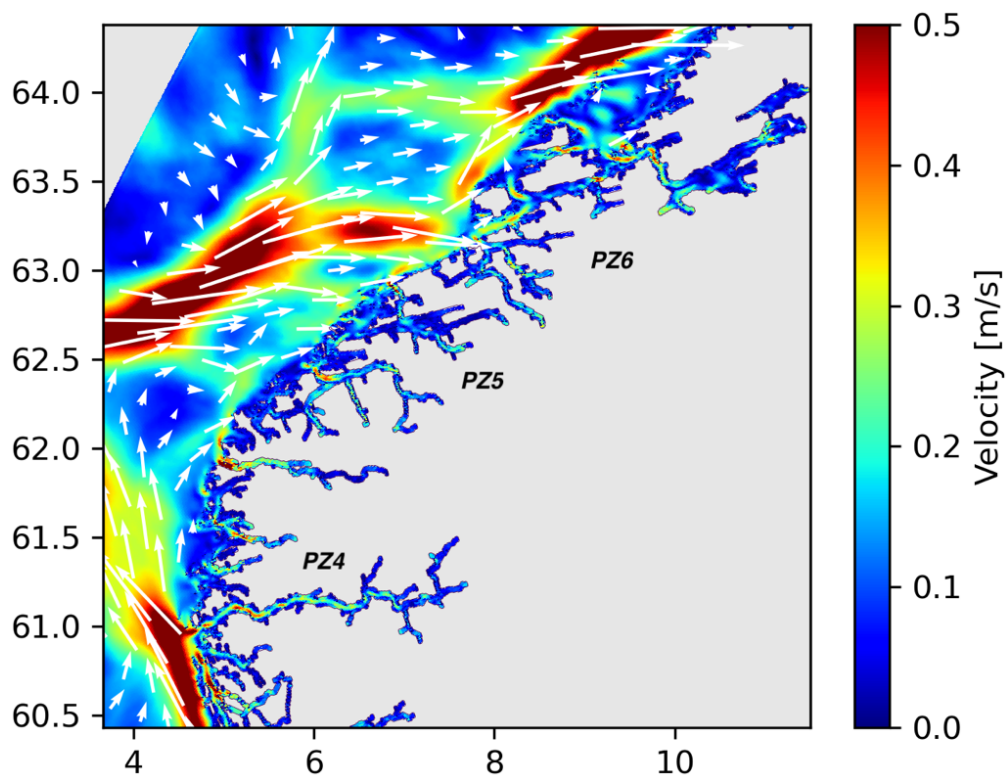

Figure 2.4: Current speed and direction of the surface water of the Norwegian coast covering PZ4, PZ5 and PZ6.

2.2 - Biological Physical Dispersal Model

To examine infestation networks and connectivity of infective pelagic lice between farms, we used an existing biological physical dispersal model. The model estimated the dispersal of salmon lice in response to oceanographic data, representing both physical properties of the ocean, and biological factors, including temperature-development and vertical movement of simulated lice. The model was run over the study period of 01.06.2017 – 01.06.2021, consisting of 2 production cycles of salmon farming. The model was executed with the inclusion of historical production data to analyse the realistic infestation network. The model output was then analysed in RStudio. The following paragraphs will describe the model further.

2.2.1 - Hydrodynamic Ocean Model

A hydrodynamic model was used to represent ocean current, temperature and salinity, which is an implementation of the Regional Ocean Model System (ROMS). ROMS is a free-surface, hydrostatic, primitive equations, general ocean model (http://myroms.org), more details in Shchepetkin and McWilliams (2005). The model was run with a horizontal resolution of 160 x 160, and 35 vertical layers of depth-varying spacing with an increasing resolution towards the surface. Between each production zone the horizontal resolution was 800 x 800. For detailed description of the model and the set up that was used, see Huserbråten and Johnsen (2022).

2.2.2 - Lice Dispersion Model

To realistically simulate the dispersal of pelagic salmon lice, a particle advection model, using an individual based model approach, was implemented to the hydrodynamic model (Huserbråten et al., 2020a). The advection of particles was modelled by the Runge-Kutta second order method, where each particle represented salmon louse, and its movement with the modelled ocean currents. The individual based model applied realistic salmon lice behaviour and properties based on existing knowledge of salmon lice biology (Chapter 1.2). The particles were for instance given the ability to move vertically in response to temperature, salinity and light. Salmon lice behaviour, mortality, individual environmental response and development were implemented as described in detail in Sandvik et al. (2020). All farms were assumed to be potential habitat for copepodids settlement. The lice dispersal model took solely copepodids

originated from lice on farmed salmonids into account, and other salmon lice sources, such as wild salmon populations, were not included in the model.

2.2.3 - The Connectivity Matrix

To calculate the potential salmon lice infestation between farms, we based the analysis on the geographical coordinates of each super-particle generated from the particle advection model. A super-particle is defined as a group of individual particles with similar properties to ensure computational feasibility (more details of the super individual approach in Scheffer et al. (1995)). If super-particles drifted within a 160 m radius around farms (nine grid cells in the hydrodynamic model) a proportion of the infective lice, represented by the super-particle, settled within the farm (Huserbråten and Johnsen, 2022). The infection rate of each super-particle varied with temperature and age in which the particle experienced, as described in Skern-Mauritzen et al. (2020).

The integrated number of modelled infective pelagic salmon lice (hereafter referred as lice infestation number) originating from farm 1 infecting farm 2, 3, 4 … 1002 and from farm 2 infecting farm 1, 3, 4 … 1002 etc. was registered for all 1002 farms in Norway (including farms beyond the study area). The integrated infestation number exchanged between farms was stored in a 1002 x 1002 matrix for every day during the study period, hereby referred to as the "Connectivity Matrix". Each element in the matrix represented the average infestation number between two farms. To create a realistic infestation network, historical production data was implemented into the model. The model used the weekly number of salmon lice and the monthly number of fish reported by the farmers at each farm, in which they are required by law to report (Chapter 1.4). Farms with zero fish, did not receive salmon lice infestations in the model, thus emphasizing lice infestations induced by salmon farming production. The farms had intersecting production in time, meaning only farms that produced fish at the same time had the potential of connectivity. Each farm has a unique farm location number, which is officially available data in the Aquaculture Register, forming the first column and first row of the matrix. The matrix thus included the total bidirectional transmission of infectious pelagic salmon lice between each pair of farms. The connectivity matrix was generated in a R-script provided by the IMR at start of the study (I. Johnsen, pers. comm., June 2023)

2.2.4 - Identifying Emergent Clusters

All 1002 salmon farms in the network were grouped into clusters based on infestation and connectivity between farms, derived from the connectivity matrix, as described in Huserbråten and Johnsen (2022). The infestation dispersal is higher within a cluster than between the clusters (Huserbråten et al., 2020a). This indicate that farms within the same cluster are more closer connected to each other compared to farms in different clusters (Huserbråten et al., 2020b).

To structure the community network and to identify clusters based of the connectivity matrix, the algorithm "infomap" was used. The algorithm is available in the R-package "igraph". This algorithm minimizes the expected description length of a random walker trajectory within the connectivity matrix (Rosvall and Bergstrom, 2008). Clusters generated by infomaps are identified by tracking how often simulated random walkers stay within certain areas, using the weighted connections in the connectivity matrix (Huserbråten and Johnsen, 2022). For further description of the theoretically framework, see Rosvall and Bergstrom (2008). Clustering salmonid farms have been done in previous studies using different algorithms, see Samsing et al. (2017) and Huserbråten and Johnsen (2022).

Here, we define a real cluster as a group of farms consisting of minimum two farms. A small cluster is defined as a cluster with two or three farms. Clusters comprising only a single farm were farms that were not actually assigned to any cluster and were referred to as false clusters. The emergent clusters were identified in a R-script provided by the IMR at start of the study for further analysis in this thesis (I. Johnsen, pers. comm., June 2023).

2.2.5 - Fjord Index

An artificial fjord-index was implemented to the lice dispersion model to calculate the farms´ locations and their distance to sea. The fjord-index resolved 800m x 800m horizontally grid. All grid-cells in open ocean, defined as > 10 km away from any land cell in the model, were assigned a value of zero. The remaining cells in open sea were initially undefined. Subsequently, the index was iteratively defined whereby undefined cells adjacent to a cell with value i got the value $i + 1$. This process was repeated until all sea cells were defined. The fjord index was utilized to create a data frame containing the farm location number and its distance to sea in a python script. This made it possible to explore the correlation between

farm isolation (Chapter 2.4), and the farm´s distance to the open sea. For further details of fjord index, see (Johnsen et al., 2021)

2.2.6 - Farm Data Output

Farm location number, cluster number, production zone number, and longitude and latitude coordinates were made as output by the above-described method from the bio-physic model. The data was uploaded in R, and further used to analyse the connectivity matrix, and to select farms from different production zones in correspondence to the study area. The output data file was referred as the farm location file.

2.3 - Network Analysis

The resulting connectivity matrix, clusters, and the farm location file generated from the bio-physical model were analysed in RStudio using R programming language and relevant functional R-packages.

2.3.1 - Quantifying Infestation

The generated connectivity matrix was used to quantify the total, internal and external infestation of each farm in the study area. The total infestation imported to a farm was quantified as the sum of each column in the connectivity matrix. The sum represented the total number of salmon lice imported to the farm, originating from external farms and from itself. The total infestation exported from a farm was quantified as the sum of each row, which accounted for the total number of salmon lice exported from a farm to surrounding farms, and lice exported to the farm itself. The total infestation numbers (imported and exported) were then saved along with the corresponding farm location number in a data frame. In this study, we refer total lice import as the total infestation number.

The total infestation number included total internal infestation, defined as the infestation a farm imported and exported to itself. Internal infestation was represented as the diagonals of the connectivity matrix. The diagonals were retrieved along with the location number to represent internal infestation of each farm and were put into a collective data frame. The external infestation was calculated as the total infestation number subtracted with the internal infestation

number. External infestation was defined as the number of lice infestations a farm received from other farms with internal infestation excluded.

The infestation numbers (total and internal) were then merged with the farm data output, making it possible to plot and map the farms. The same procedure was performed for all three PZs in our study area. The total infestation numbers were calculated using R-programming language, default packages, and functional R-packages; including "dplyr" for data manipulation tasks, and "readr" to read large datafiles efficiently.

A linear regression model was used to explore correlations in RStudio, and to calculate the p-value and R-squared value (R^2). The correlation between total infestation imported to a farm and total infestation exported from a farm was examined. The correlation between internal infestation and external infestation was also examined. The linear regression analysis was performed using the R-function "lm" to generate the linear model and "summary" to summarise the results. The p-value and R^2 were used to evaluate the correlation significance and variance. A p-value lower than 0.05 was considered a significant correlation, and the R^2 value measured the proportion of variance in the dependent variable that is explained by the independent variable, and how close the data was to the fitted regression line. Linear modelling plots were also generated using R-programming language and the R-packages "ggplot2", "scales", and the base package "stats" to create a scatter plot to visualise the correlations.

2.3.2 - Quantifying Connectivity

The connectivity matrix was used to quantify connectivity between farms in each cluster. Connectivity between farms were defined as the number of lice (or infestation) exported and imported (transferred) from one farm to another and represented the lice dispersal potential. Connectivity for each farm was quantified by retrieving the lice infestation numbers between farms in the connectivity matrix.

The connectivity was quantified by sequentially iterating through the connectivity matrix in RStudio using for-loops and default R-packages. The R-code was extracted the bidirectional connectivity between all farms and stored the data in a csv-file. The resulting connectivity csv-file contained the connectivity (number of lice) between farm 2 moving to farm 1 for all farms.

The connectivity csv-file was then sorted using "dplyr" R-package to identify farms that belonged to the correct production zone within the study area. The connectivity numbers were integrated into a collective data frame, which included farm location number, cluster, production zone, longitude and latitude. This enabled effective mapping of each farm and the connectivity between them. High connectivity meant a large number of lice transferring between two farms. To optimally visualize the connectivity and to enable comparison of each production zone, we selected the top 800 strongest connections for all three PZs. We defined top 500 connections as strong, and the remaining 300 connections as weak, and excluded the rest.

2.3.3 - Cluster Analysis

Total lice infestation was calculated for each cluster. This was done by arranging the farm lice infestation numbers according to cluster and summarizing the individual lice infestation numbers for each farm in the clusters. The total lice infestation thus was the total number of lice imported to each cluster. The internal infestation of each cluster was defined as the infestation a cluster imported and exported to itself. Thus, the collective internal infestation was calculated as the internal infestation of each individual farm and the total number of lice transferring between internal farms within the cluster. The summarized data was stored in a new data frame containing cluster, location number, total- and internal infestation numbers, making it possible to plot and visualize the clusters of farms, and map the infestation network. The number of clusters and the number of farms in each cluster were also quantified and stored in R. The total infestation of each production zone was calculated by summarising each cluster´s total lice infestation. The total lice infestation thus was the number of lice imported to all the clusters within each PZ, and external infestation from different PZ was excluded. The correlation between the number of farms and the total lice infestation of all 13 PZs in Norway were examined in R using the same linear model as previously described.

Visualizations of the infestation network and connectivity between farms, were created using "ggplot2", "ggmap", "ggOceanMaps", "ggspatial", and "rnaturalearth" R-packages. Maps were generated to present the locations of the farms, and to illustrate the infestation pressure of each farm and cluster. The same legend scales were used to ensure an accurate comparison across the three production zones in the study area.

2.4 - Calculating the Isolation Ratio

To assess the extent of isolation of each cluster and farm we calculated the isolation ratio. The cluster isolation was though the primary focus in this study. The isolation ratio was defined as the ratio between internal infestation and total infestation (Equation 1).

$$\textit{\textbf{Equation 1}} \qquad Isolation\ ratio = \frac{internal\ infestation}{total\ infestation}$$

Here, the term "isolation" was defined as the percentage of internally sourced lice infestations. For instance, an isolation ratio of 80% indicated that 80% of the total infestation was internally sourced in the respective farm or cluster. An isolation ratio of 1 (or 100%) implied that the internal infestation was equal to total infestation, and that the only infestation a farm received was internally sourced. Conversely, an isolation ratio of 0 implied that a farm only had lice infestation sourced externally. The farms with a total infestation value of 0 were excluded from the calculations, as the isolation ratio was not possible to quantify. This was a total of 47 farms in the study area. The same linear regression model as earlier described was used to investigate the correlation between the farm´s isolation ratio and their distance to open sea using the fjord index.

The isolation ratio of each cluster was calculated using the ratio of total internal infestation within a cluster and total infestation within a cluster. Lastly, the clusters were mapped to examine geographic patterns related to the infestation numbers and the isolation ratios. The R-packages used were "ggplot2", "ggmap", "ggOceanMaps", "ggspatial", and "rnaturalearth" to generate visualisations. The same procedure was done for all production zones in the study area. The same legend scales were used to ensure an accurate comparison across the three production zones.

2.5 - Isolating the Clusters in the Infestation Network

To explore the possibility of further isolating the clusters in the infestation network, we analysed the cluster´s external infestations. The external infestation sources and the internal infestation recipients were identified. Bar charts were made to visualize the top 20 external infestation

sources and internal infestation recipients that each farm had, and their infestation contribution to the cluster.

To investigate the possibility of further isolating the clusters in network, we wanted to calculate the effect of removing farms, and see how the isolation ratio responded. Only external farms were removed. The external farms were arranged according to the number of lice they transferred to the cluster. The external farms with highest infestation were removed first. A R-script using for-loops was created that removed farms sequentially. The loops were constructed to remove up to 20 external farms. The cluster´s isolation was calculated for each farm removed. The new isolation ratio after removal was calculated as the ratio between the cluster´s internal infestation and the cluster´s total infestation subtracted with the external infestation removed. The R-package "dplyr" was used for these data manipulation tasks.

The R script generated a new data frame containing cluster number, the isolation ratio and the number of external farms removed. To visualize the effect of removing farms on the isolation ratio, a plot of isolation ratio and number of external farms removed was created. A plot of the relative change in the clusters´ total infestation was also made. The same procedure was repeated for each production zone.

3   Results

This chapter will present the results of the study, where lice dispersal and connectivity were quantified using a biologic physical dispersal model. The realistic infestation network was visualized for three production zones in Norway: PZ6, PZ5 and PZ4. Emergent clusters served to fragment the infestation networks. The isolation ratios of individual farms and clusters were quantified, and the possibility of further isolating the clusters in the infestation network investigated.

3.1 - Infestation Network, Clusters and Farm Connectivity

The clusters were previously identified based of the connectivity matrix. The clusters formed a significant component of the infestation networks. The 141 farms located in PZ6, was grouped into 32 clusters, where only 5 were classified as real (Table 3.1). The clustering thus resulted in 27 false clusters, which was the highest number of all three PZs. The clusters were also largest in PZ6, where the number of farms per cluster ranged between 1 and 54, with an average of 23 farms per real cluster. In PZ5, a total of 27 farms were grouped into 9 clusters. However, 6 of these clusters were defined as false, leaving only 3 classified as real clusters (Table 3.1). The clusters of PZ5 and PZ4 encompassed fewer farms, where number of farms ranged from 1 to 22 farms in PZ5. On average, there were 13 farms per real cluster. In PZ4, the number of farms per cluster ranged between 1 and 31, with an average of 14 farms per real cluster. In total, there were 138 farms, which partitioned into 22 clusters. Of these, 9 were classified as real clusters (Table 3.1). In addition, five clusters were defined as small, and 13 were identified as false clusters in PZ4. In all three PZs, the false clusters composed of 7 farms that did not produce fish at all during the study period, while 25 farms did produce fish at some point during the study period.

Table 3.1: Overview of clusters in PZ6, PZ5 and PZ4.

	Number of farms	Emergent clusters	Small clusters	False clusters	Real clusters
PZ6	141	32	0	27	5
PZ5	46	9	0	6	3
PZ4	138	22	5	13	9

The analysis of the connectivity matrix generated multiple maps of the infestation networks (Figure 3.1-3.3). These maps provided an overview of the entire connectivity infestation network across the study area. The connectivity is represented with arced blue lines, displaying the transmission of lice between farms. For clarity, only the top 800 connections were selected across the entire study area. The strongest 500 connections are represented with a dark blue colour, while the remaining 300 relatively weaker connections display a lighter blue colour.

The infestation network of PZ6 comprised large clusters (Figure 3.1a). The clusters encompassed primarily open coastlines, but also some smaller fjords. The infestation pressure was relatively low across the entire PZ, with no large-sized farms particularly standing out. The lice infestation pressure was consistent in clusters located both fjords and in open coastal areas. There were strong connections observed throughout the PZ, with the strongest connections occurring among farms within the same cluster. Strong connectivity was observed within clusters located in fjords and in open coastlines. The connectivity between farms spanned both over large and short distances. The direction and extent of lice dispersal varied from cluster to cluster. Cluster 2 was large, and thus had the longest lice dispersal distance across all three PZs. Lice travelled over large geographical areas, affecting farms located far away within the cluster. The connectivity lines were strong throughout cluster 2, with lice exhibiting a northern dispersal drift. Conversely, cluster 23 had densely populated farms located in close proximity to one another. The connectivity lines within this cluster were strong but with mostly internal lice transmissions and short lice dispersal distances. Cluster 17, located in the northern part of the zone, lice drifted in a southern direction, unlike in cluster 2. In cluster 22, lice mostly moved inward along the fjord.

The infestation network of PZ5 were divided into three parts by the clusters (Figure 3.1b). These clusters were relatively smaller, and encompassed both fjords, and open coastlines. Cluster 25

had the highest lice infestation pressure in PZ5, with the largest circles observed in the southern part of the PZ. There were fewer connectivity lines in PZ5 compared to PZ6 and PZ4. The strongest connections were predominantly observed in cluster 25, which were located in a fjord. Cluster 12 and 41 exhibited mostly weak connections between farms, although some strong connections were also observed. The transmission of lice occurred primarily between farms in close proximity, observing shorter lice dispersal distances compared to PZ6. In open coastal areas, there was a slight northward movement of lice, particularly observable in cluster 12. In PZ6 and PZ5, there was some connectivity between farms in different clusters, but these connections were generally weak.

The infestation network of PZ4 showed that almost every cluster contained farms exhibiting higher infestation pressure than other farms (Figure 3.1c). The farms showed both higher infestation pressure, and lower infestation pressure across all PZ4. This was a contrast to the other clusters in PZ5 and PZ6, which had more consistent lice pressure among farms within clusters. The clusters emerged primarily in smaller and larger fjords, but some clusters also encompassed large open coastlines. In PZ4 and PZ5, the farms located in coastal areas and open sea, mainly showed lower infestation pressure. Conversely, the farms with relatively highest infestation pressure were primarily located in the fjords.

The connectivity network of PZ4 comprised both strong and weak connections, with the strongest connections predominantly observed in cluster 5. Within cluster 5, three farms positioned in the middle of the cluster stood out with higher infestation pressure and strong connectivity with surrounding farms. The strongest connections were observed mainly in fjords in PZ4 and PZ5. There were also strong connectivity lines linking farms across different clusters, which were not observed in PZ5 or PZ6. Specifically, a farm in cluster 16 transferred lice to farms in cluster 14, thereby connecting these to clusters. However, in general the lice moved mainly between internal farms within the clusters for all PZs. In PZ4, the transmission of lice occurred primarily between farms in close proximity, with minimal long-distance lice dispersal, in contrast to PZ6. The dispersal of lice was unidirectional, specifically in cluster 15 and 16 which were located in open coastlines, where lice tended to move in a northern direction. For clusters located in fjords, lice dispersal and connectivity patterns were multi-directional, with movements both inward and outward along the fjord. This multi-directional pattern was observed in all three PZs.
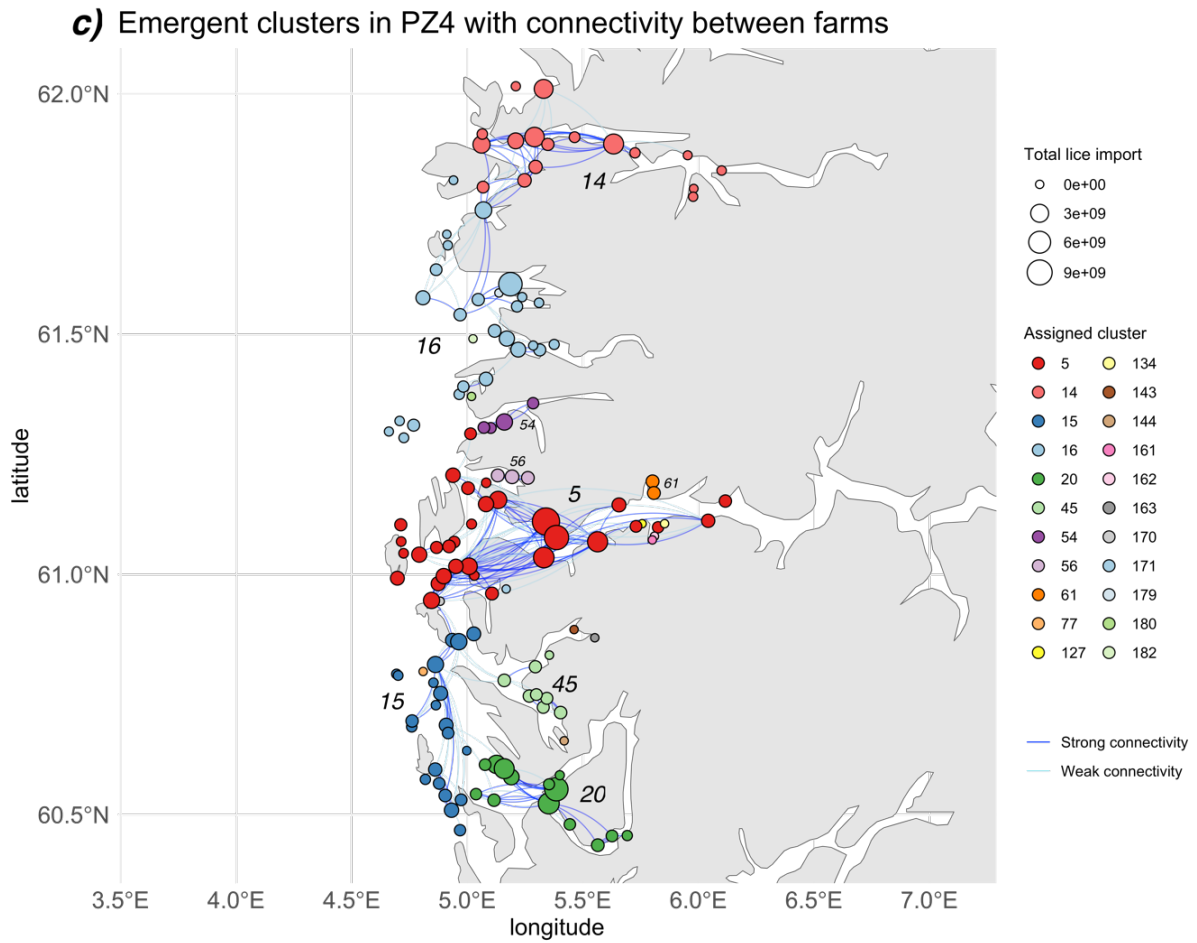
a) Emergent clusters in PZ6 with connectivity between farms

b) Emergent clusters in PZ5 with connectivity between farms
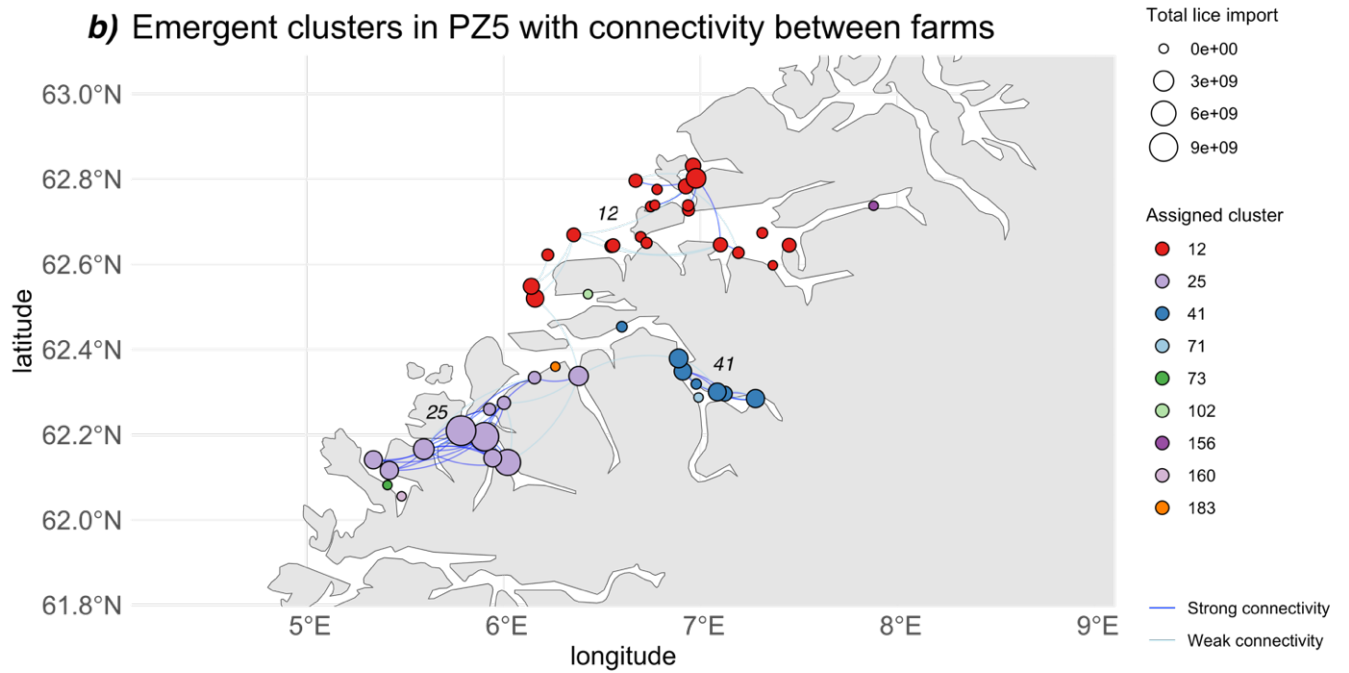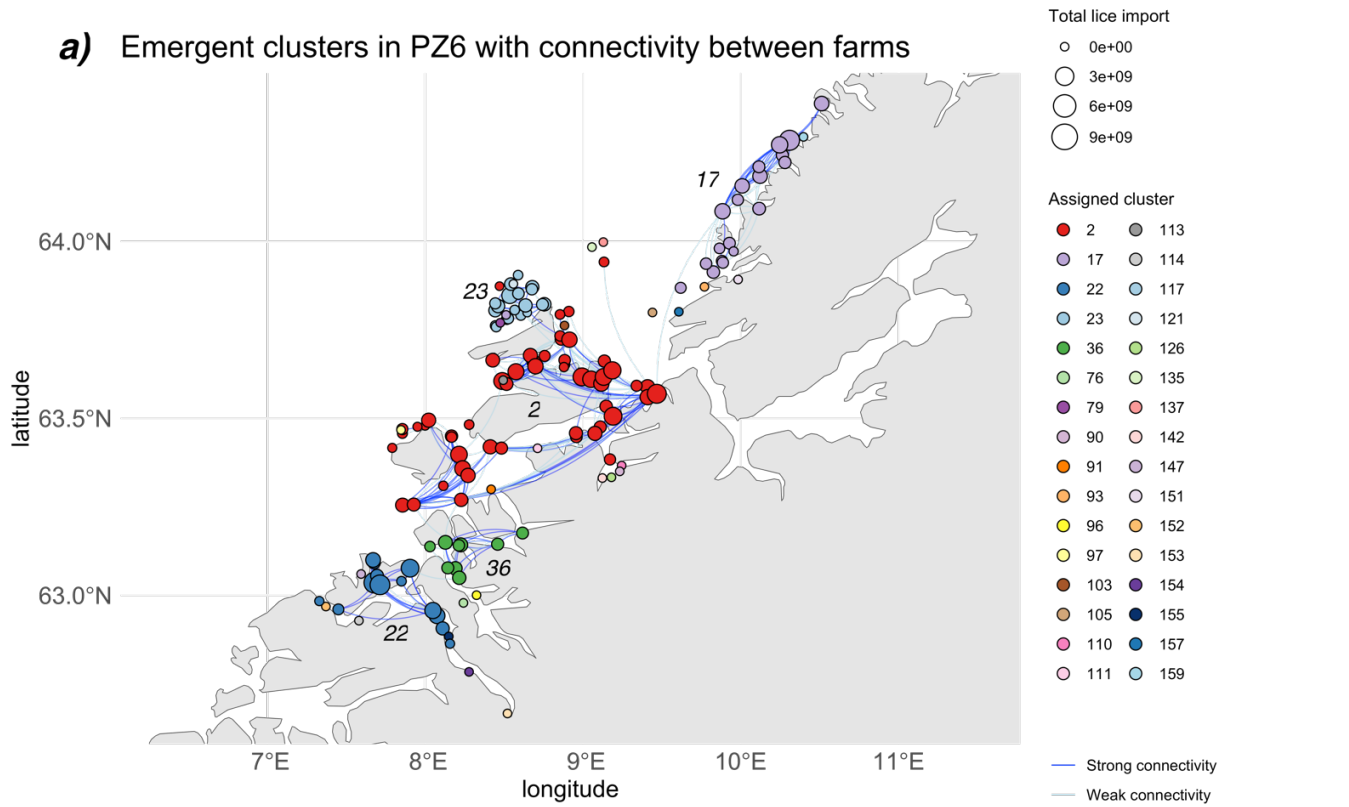
*Figure 3.1: The infestation networks of each production zone: **a)** PZ6, **b)** PZ5, and **c)** PZ4, showing clusters, total lice import of each farm, and connectivity between farms. Each circle and its colour represent farms belonging to different clusters. The circle size is scaled according to lice import, reflecting each farm's infestation pressure. Connectivity between farms is represented with arced blue lines, where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice but indicate the origin and destination of lice infestations*

3.1.1 - Total Lice Infestation of Each Production Zone

The total lice infestation of each PZ represented the total number of lice imported to each cluster in each production zone. The highest total infestation was observed in PZ4, while the lowest was observed in PZ5 (Table 3.2). However, the average infestation per farm and real cluster was highest in PZ5. PZ4 had the highest infestation pressure per biomass salmonids produced, whereas PZ6 had the lowest infestation pressure per biomass. PZ6 had also the lowest average infestation per farm of all three PZs.

Table 3.2: Total lice infestation imported to all clusters, average lice infestation of each farm, average lice infestation of each cluster, and total lice infestation per biomass of salmonids in PZ4, PZ5 and PZ6.

	Total lice infestation (number of lice)	Average lice infestation per farm	Average lice infestation per real cluster	Average lice infestation per biomass of salmonids
PZ4	135 059 106 188	986 087 214	16 006 567 354	1 662 727
PZ5	59 497 852 871	1 293 420 649	19 832 617 624	1 369 139
PZ6	88 467 637 976	627 466 974	17 693 527 595	598 528

The linear regression model revealed a positive and significant correlation (p-value < 0.01, R^2 = 0.455) between the number of farms and total lice infestations for all 13 PZs in Norway. The total lice infestation was higher with higher number of farms present in each PZ. Additionally, the correlation between lice import and lice export at farms across all PZs in Norway revealed a strong positive correlation, where farms with higher lice import was associated with higher lice export, and vice versa (p-value < 0.001, R^2 = 0.912) (Appendix A, Figure 7.1).
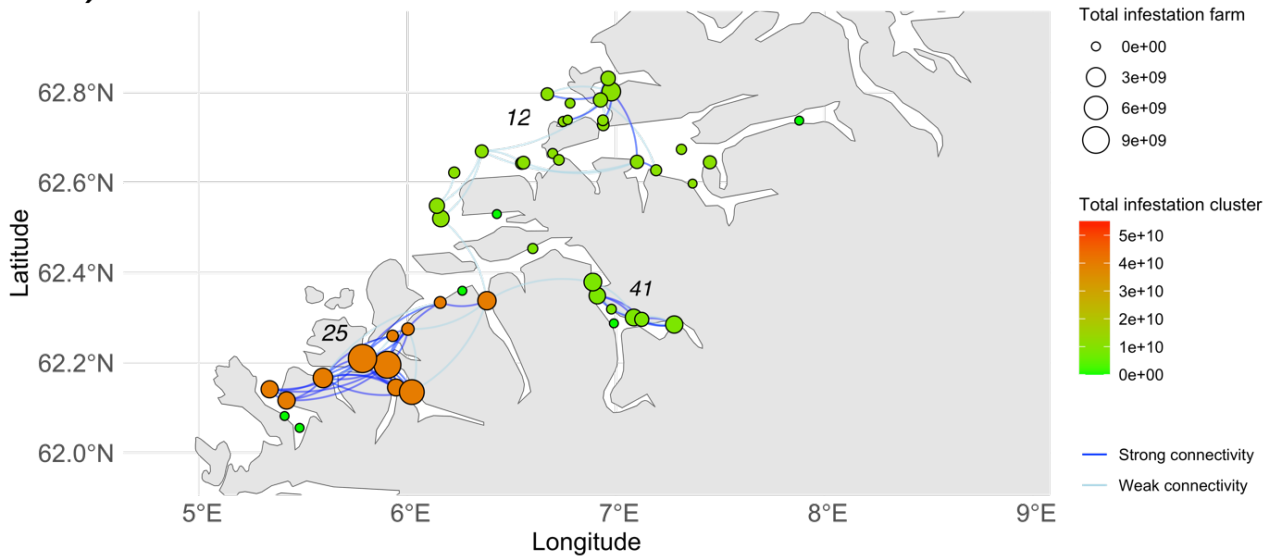
3.1.2 - Total Lice Infestation of Each Cluster

The infestation networks of all PZs revealed variability in infestation pressure among clusters, with some experiencing higher pressures and other lower pressures. Cluster 5 was distinctly recognized as the cluster with highest total lice infestations of all PZs (Figure 3.2c). Each PZ had one cluster standing out with higher infestation than the other clusters. Cluster 2 had the highest lice infestation pressure in PZ6 (Figure 3.2a), while cluster 25 had the highest infestation in PZ5 (Figure 3.2b). The rest of the clusters exhibited relatively lower infestation pressures. The false clusters showed 0 lice infestations in all three PZs.

a)   Total lice infestation of each cluster in PZ6
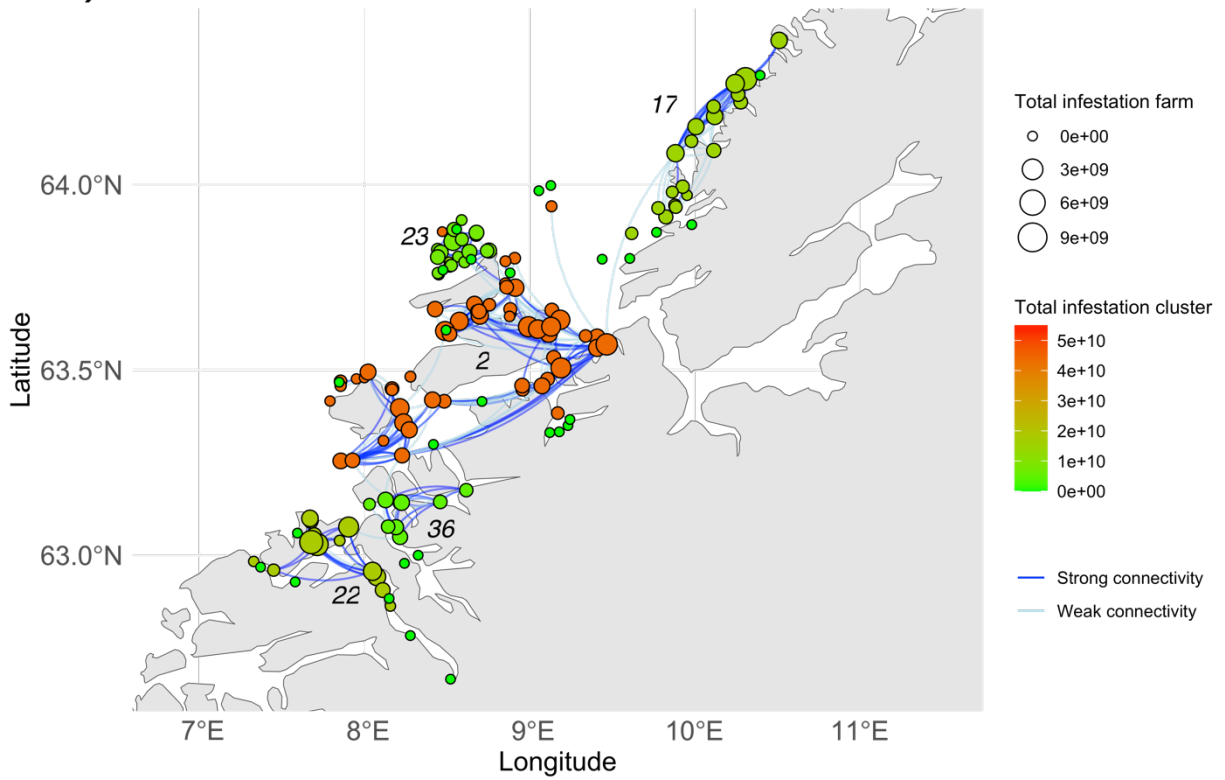
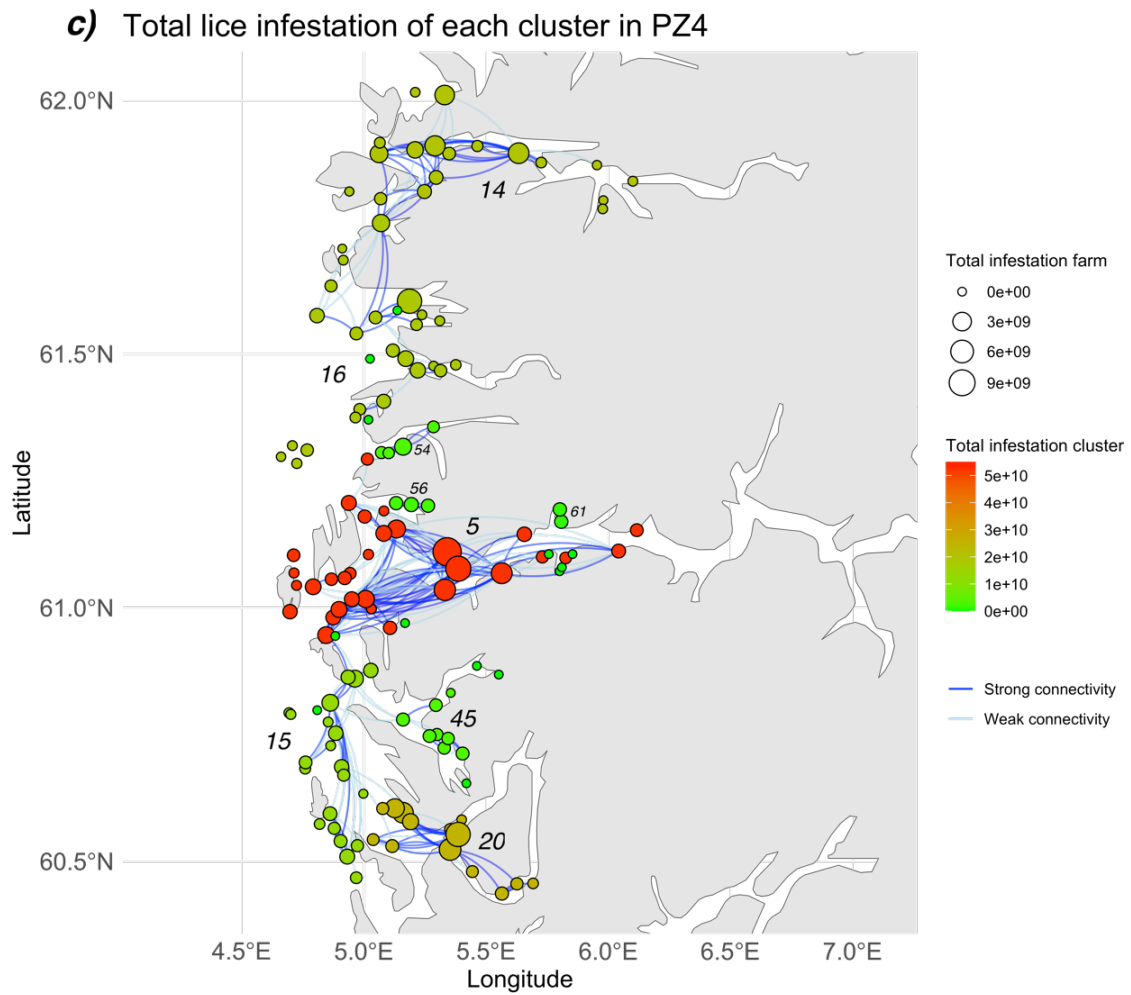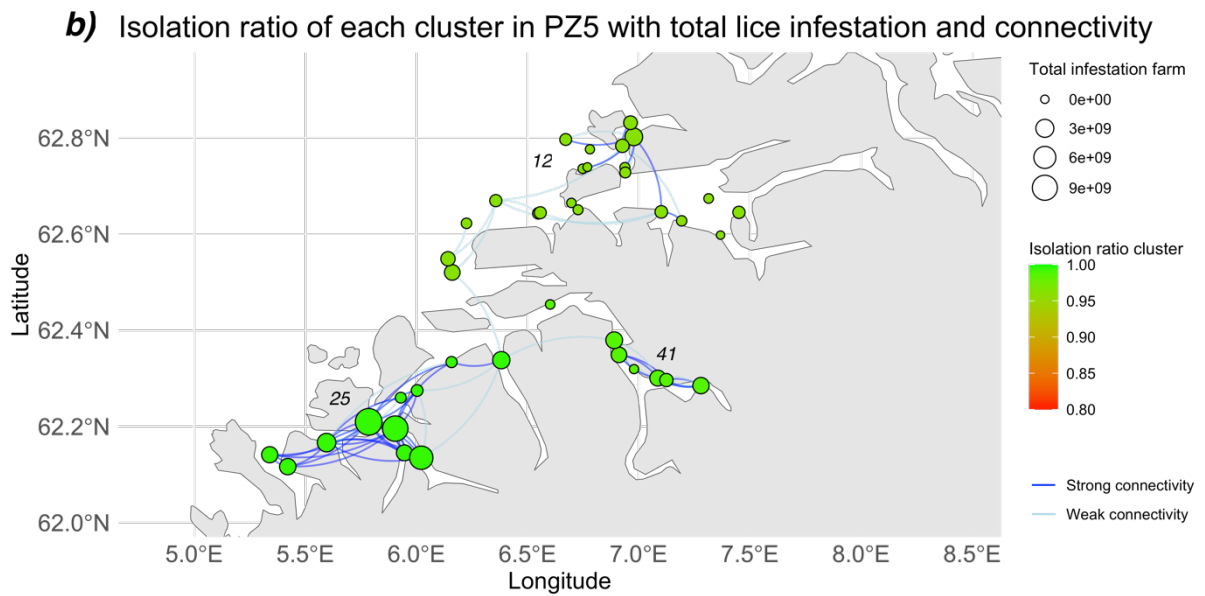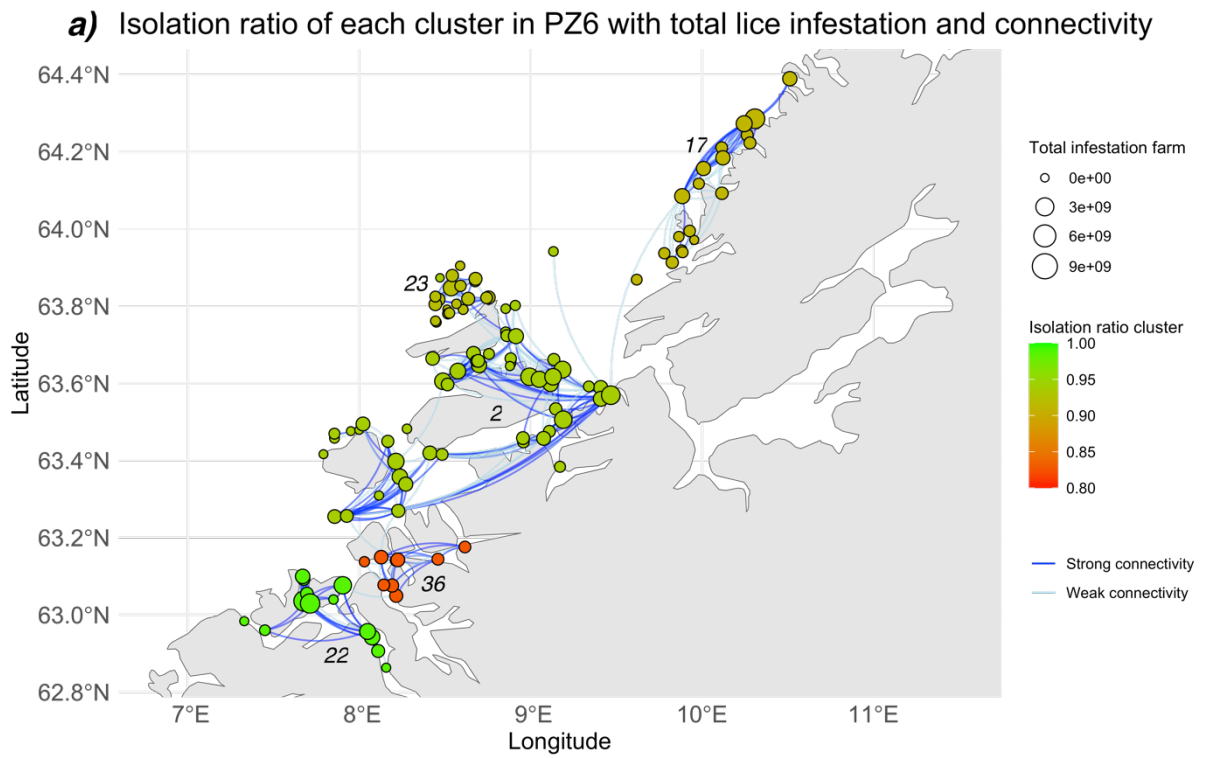**b)**   Total lice infestation of each cluster in PZ5

*Figure 3.2: The infestation networks of **a)** PZ6, **b)** PZ5, and **c)** PZ4, presenting total lice infestation of each cluster, with total lice infestation of each farm (lice import), and the connectivity between them. Circles represent farms where the small number represents the cluster number. The circle size is scaled according to lice import, reflecting each farm´s infestation pressure. The colours represent the infestation pressure of each cluster collectively and are scaled from green to red, reflecting low to high infestation pressure. Connectivity between farms is represented with arced blue lines where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice.*

3.2 - Isolation Ratio of Each Cluster

The isolation ratio was quantified for each cluster to explore to what extent the clusters in the network were isolated from each other. The isolation ratios of the clusters across all three PZs were generally high (Figure 3.3a-c). The most isolated clusters were found in PZ5, with an average isolation ratio of 0.981. Clusters in PZ4 and PZ6 showed relatively lower and similar isolation ratios. In PZ6, the cluster isolation ranged from 0.827 to 0.986 with an average isolation ratio of 0.917. Similarly, the cluster isolation in PZ4 ranged from 0.824 and 0.986, with an average of 0.914.

The infestation networks of PZ6 and PZ4 displayed variable isolation ratios among clusters. The infestation network of PZ5 presented highly isolated clusters, where cluster 25 had the highest isolation ratio of 0.995 across all three PZs (Figure 3.3b). Cluster 36 in PZ6 and cluster 56 in PZ4 had the lowest isolation ratios across all three PZs (Figure 3.3a, c). These clusters were all located within fjords. The highest isolation ratio in PZ6 was observed in cluster 22, while the highest isolation ratio in PZ4 was found in cluster 20. These two clusters were also located within fjords. The cluster isolations thus revealed that clusters located within fjords could exhibit both high isolation ratios, but also lower isolation ratios. In open coastal areas there was varying extent of cluster isolation. Cluster 2 in PZ6 had relatively high isolation ratio, but cluster 15 in PZ4 had lower isolation ratio. In all three PZs, there was no observable difference in cluster isolation from southern to northern regions.

Some clusters demonstrated both relatively high isolation ratios and high total infestation pressures, such as cluster 2 in PZ6 and cluster 5 in PZ4. These clusters were relatively large and covered a large area. Cluster 25 in PZ5 also showed high infestation pressure and high isolation ratio.

a) Isolation ratio of each cluster in PZ6 with total lice infestation and connectivity

b) Isolation ratio of each cluster in PZ5 with total lice infestation and connectivity
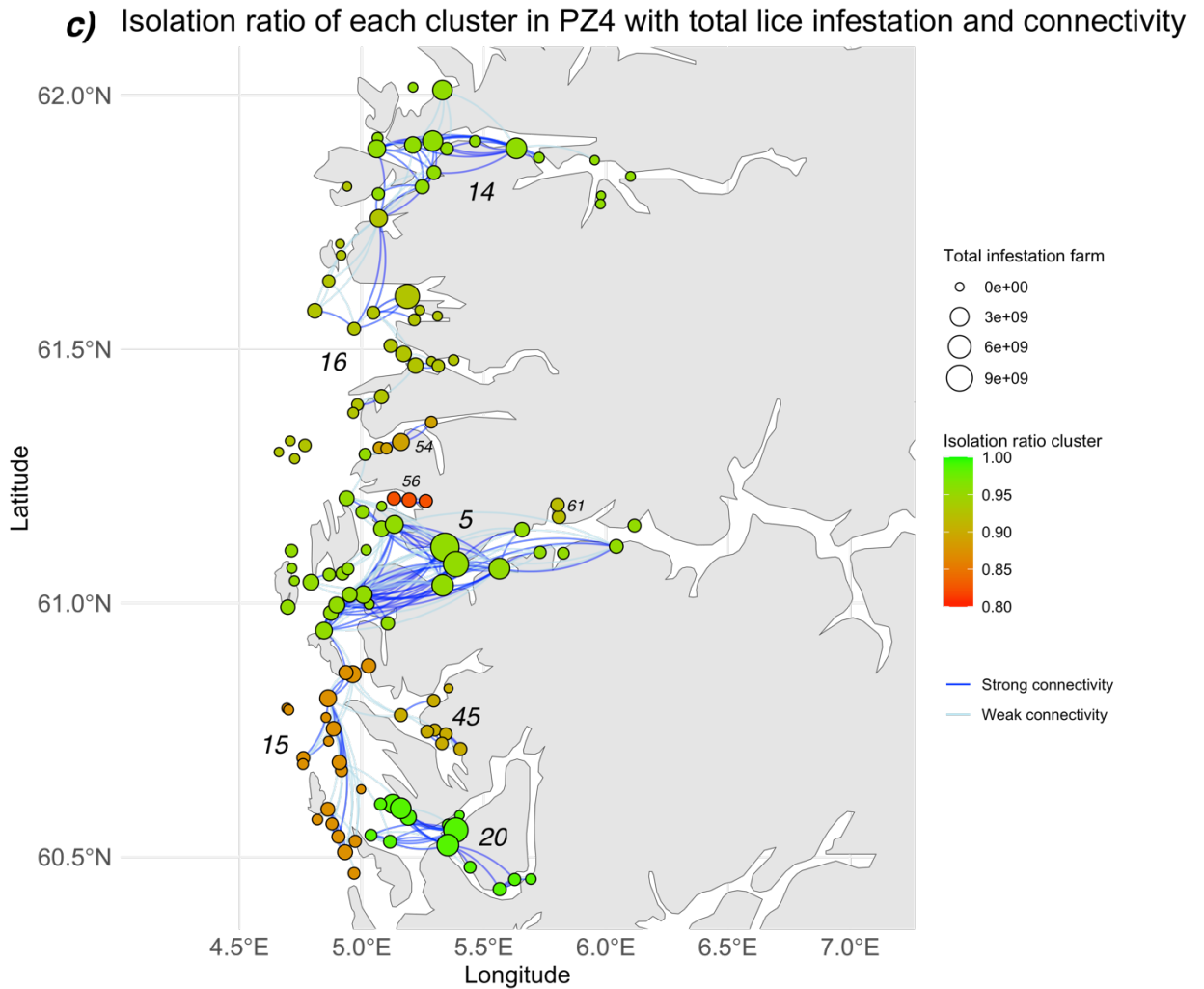
*Figure 3.3: The infestation networks of **a)** PZ6, **b)** PZ5, and **c)** PZ4, presenting the isolation ratio of each cluster, and total lice infestation of each farm (lice import), and the connectivity between them. Circles represent individual farms located in the clusters. The small numbers represent the cluster number. The circle size is scaled according to lice import, reflecting each farm´s individual infestation pressure. The colours represent the isolation ratio of each cluster where the colours are scaling from green to red, reflecting low to high isolation. Connectivity between farms are represented with arced blue lines where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice.*

3.2.1 – Isolation ratio of Each Individual Farm

The individual farms were in general less isolated compared to the clusters (Appendix C, figure 7.3-7.5). There were high spatial variations between the farms´ isolation ratios within the clusters. All clusters had farms with both low isolation, and farms with high isolation. The isolation ratios varied from 0.008 to 0.863 in PZ5, and 0.002 to 0.963 in PZ4. PZ6 displayed the least isolated farms, where the individual farm isolations ranged between 0 and 0.740. The isolation ratios remained low across all farms in PZ6. Here, there were two farms with 0

isolation that were located in open coastal areas. Cluster 22 in PZ6 and cluster 5 in PZ4 had mainly farms with high individual isolation, which also reflected on their high cluster isolation.

The infestation networks of all three PZs revealed that farms with the lowest isolation were located at the coast, whereas the farms with higher isolation were located in the fjords. (Appendix C, Figure 7.3-7.5). The correlation test between the distance to open sea and the individual farm isolation ratio gave a significant positive correlation for farms in PZ4 (p-value < 0.001, R^2: 0.135), for farms in PZ5 (p-value < 0.05, R^2: 0.119), and also for farms in PZ6 (p-value < 0.01, R^2: 0.064). The individual farm isolations increased as the distance to sea increased (moving inward the fjords). However, in all three PZs there were a high proportion of unexplained variance, as indicated by the low R^2 values.

3.3 - Isolating the Clusters in the Infestation Network

The external infestation of each cluster was examined to explore the possibility of further isolating the clusters in the infestation networks. The top 20 external infestation sources and internal infestation recipients were identified for each cluster. The results revealed that all clusters showed variable number of external infestation sources and recipients across all three PZs. The external infestation originated from multiple farms, or few farms, or one primary farm, and dispersed to multiple farms, or few farms, or one primary farm. Bar charts of cluster 5, 12 and 25 are illustrated here. For additional clusters and detailed maps, see Appendix D.

Cluster 5 was located in PZ4 and consisted of 31 farms. This cluster had the highest infestation pressure in PZ4, with a high isolation ratio of 0.955. The cluster´s external infestation originated from multiple external farms, with five to six farms responsible for a significant amount of lice infestation moving to the cluster (Figure 3.4a). The external infestation dispersed to multiple internal farms, with one farm importing significantly more lice to the cluster (Figure 3.4b).

Cluster 12 was located in PZ5 and consisted of 22 farms with a cluster isolation of 0.962. The external infestation originated from multiple external farms, with one farm standing out with highest infestation contribution (Figure 3.4c). The external infestation dispersed to a small number of internal farms within the cluster. One farm stood out as the primary recipient which imported the majority of the external infestation (Figure 3.4d). Cluster 23 was located in PZ6

and consisted of 23 farms with a cluster isolation of 0.921. The external infestation originated from one primary farm and dispersed to multiple internal farms (Figure 3.4e-f).
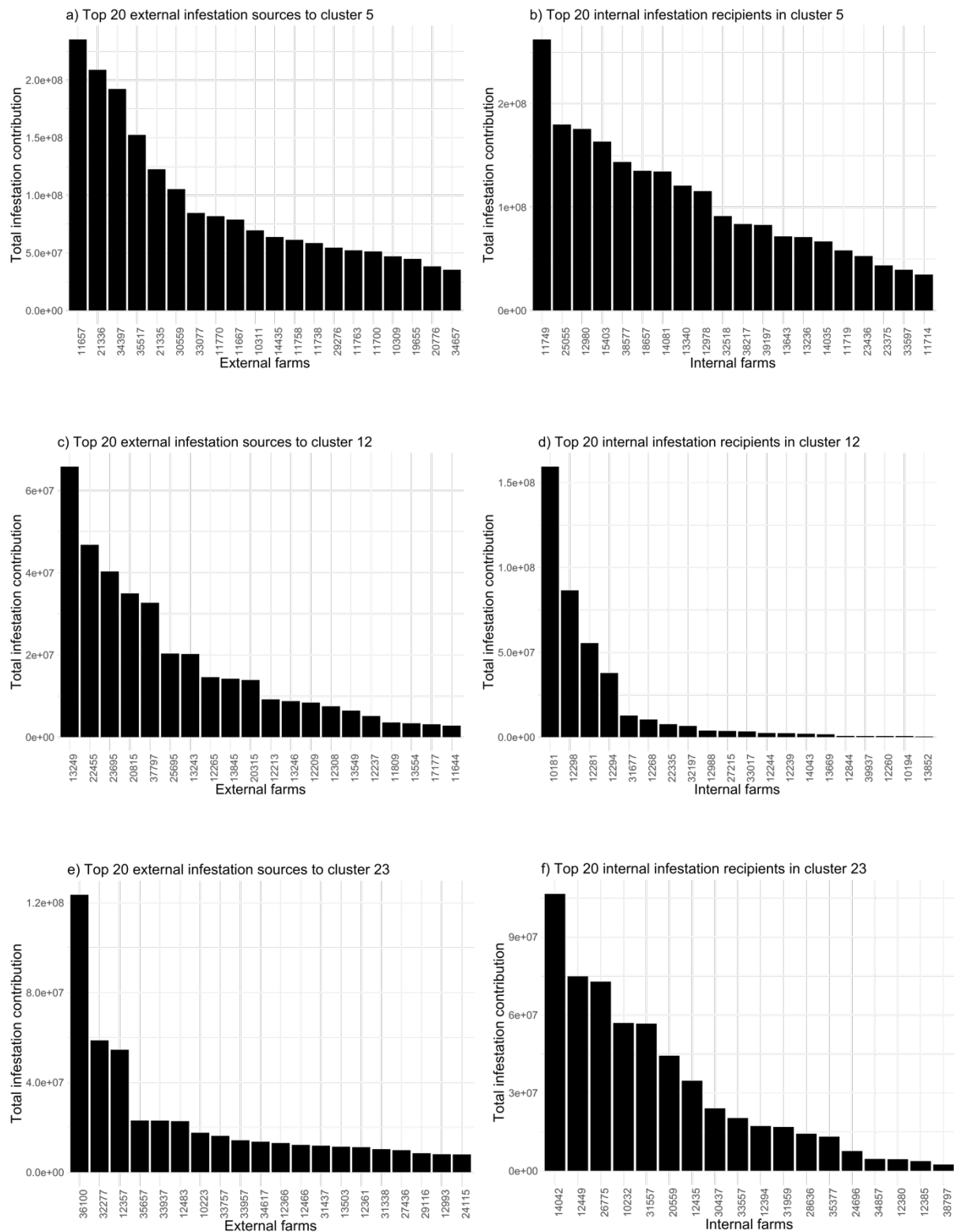

*Figure 3.4: Top 20 external infestation sources for **a)** cluster 5 in PZ4, **c)** cluster 12 in PZ5, and **e)** cluster 23 in PZ6. The top 20 internal infestation recipients are also shown for **b)** cluster 5, **d)** cluster 12, and **f)** cluster 23. One cluster was selected from each PZ in the study area. Note that the y-axis varies among the bar charts.*

Additionally, cluster 2 in PZ6 and cluster 45 in PZ4 were examined. The external infestation in cluster 2 originated from multiple farms and dispersed to multiple internal farms (Appendix D, Figure 7.9). The external infestation of cluster 45 originated from few farms and dispersed to one primary internal farm (Appendix D, Figure 7.11).

3.3.1 - The Effect of Removing Farms on Isolation Ratio and Total Lice Infestation

The effect of removing external farms on isolation ratio and total lice infestation was examined to potentially isolate the clusters in the infestation networks even further. The isolation ratio increased as more external farms were removed for each cluster in all three PZs (Figure 3.5a, c, e). Most clusters approached a value of 1, which demonstrated that the removal of up to 20 external farms created almost fully isolated clusters. Some clusters had rapid increase in isolation with the removal of fewer external farms. Other clusters exhibited a slower increase in isolation and required more farms to be removed to achieve a higher isolation. Some clusters became almost 100% isolated. These were cluster 22 in PZ6, cluster 25, and 41 in PZ5, and cluster 14 in PZ4. These clusters were all located in fjords. The clusters that achieved the lowest isolation after removal of 20 farms were respectively cluster 15 in PZ4, cluster 36 and cluster 17 in PZ6. Cluster 15 and 17 were located in open coastlines, but cluster 36 was located in a fjord. The clusters with few external infestation sources increased the isolation with the removal of fewer farms than clusters with multiple external infestation sources. Both cluster 23 and cluster 45 had few external infestation sources, and the isolation rapidly increased when removing external farms (Figure 3.5 a, e). Cluster 2 on the other hand, had multiple external infestation sources and a slower increase in isolation (Figure 3.5a).

The total lice infestation decreased as more external farms were removed for each cluster in all three PZs (Figure 3.5b, d, f). The greatest decrease in total lice infestations for all PZs were shown in cluster 36 in PZ6 and cluster 56 in PZ4. The lowest change in total lice infestations for all PZs were observed in clusters that had highest isolation initially before removal of external farms. These clusters were cluster 22 in PZ6, all clusters in PZ5, and cluster 20 in PZ4 (Figure 3.5).
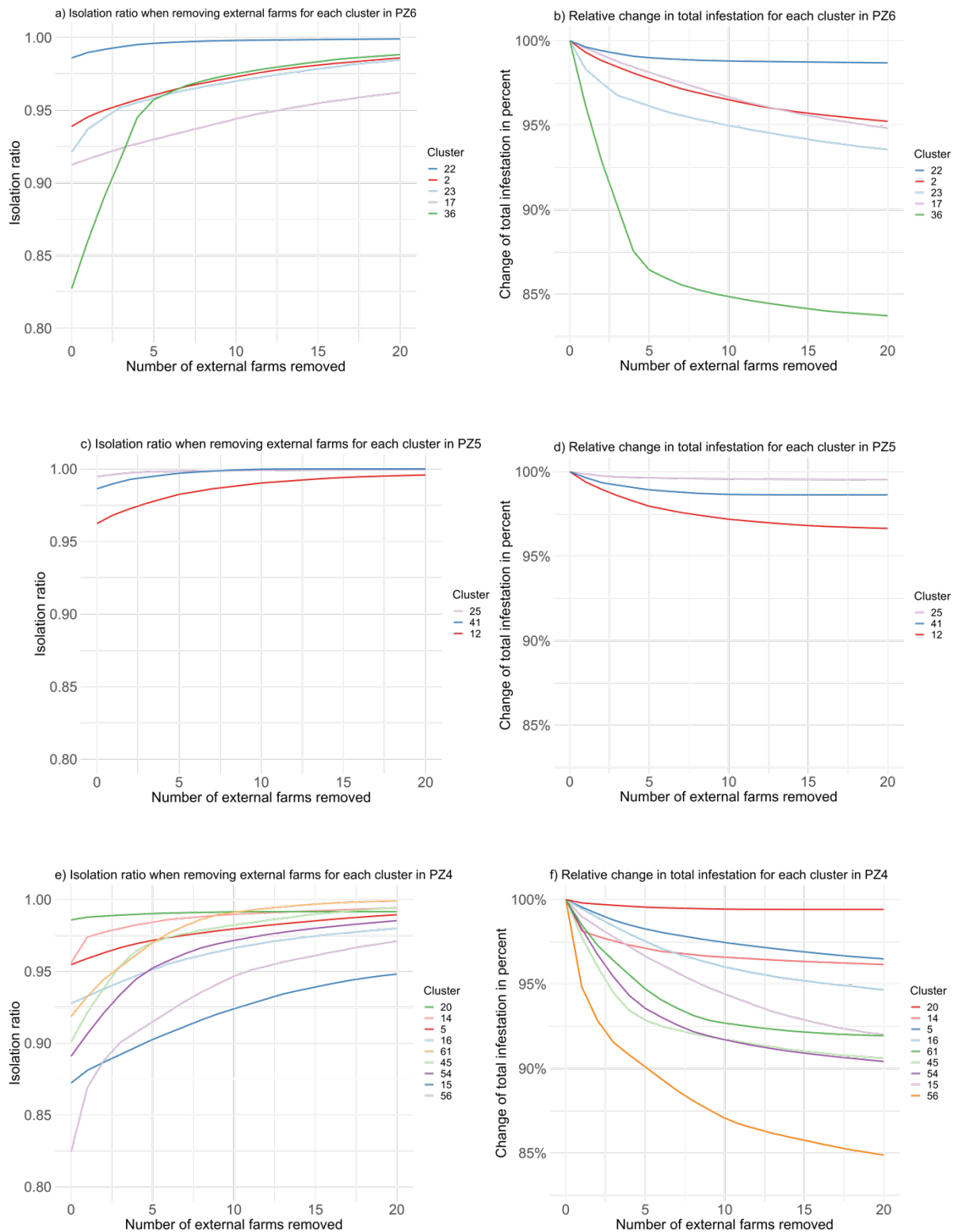
*Figure 3.5: The isolation ratio when removing a total of 20 external farms for each cluster in **a)** PZ6, **c)** PZ5, and **e)** PZ4. The relative change in total infestation for each cluster when removing a total of 20 external farms in **b)** PZ6, **d)** PZ5, and **f)** PZ4.*

4 Discussion

Effective management of lice infestations in salmon farming is essential to prevent unsustainable impacts on wild salmonid populations. Lice connectivity is influenced by hydrodynamic forces and is further complicated by the spatial arrangement of salmon farms, and the presence of hosts for salmon lice. The bio-physic dispersal model simulated the dispersal of infective pelagic salmon lice larvae, by incorporating oceanographic physics, historical production data, and lice biology, to realistically represent connectivity between farms in terms of lice infestations. A network analysis was performed, by analysing the connectivity matrix, to create fragmented connectivity infestation networks in PZ4, PZ5 and PZ6.

4.1 - Cluster Structure

The network analysis revealed highly fragmented community structures within each PZ. Clusters emerged within the community structure, organizing the infestation networks into smaller units. The clusters emerged in a way that resulted in higher infestation dispersal within clusters than between clusters (Huserbråten et al., 2020a). Clusters of farms may represent alliances for collective management efforts (Samsing et al., 2017). Coordinated management of lice treatments and fallowing periods have the potential to reduce lice infestations and treatment frequency (Arriagada et al., 2017; Murray and Salama, 2016; Stige et al., 2024).

Generally, the clusters in PZ6 were larger than clusters observed in PZ4 and PZ5. The larger cluster size in PZ6 can be attributed to its extensive coverage of sea area, characterized by open landscapes with fewer narrow fjords and more open coastlines, as observed in cluster 2 and 17. This geographical configuration facilitated the dispersal of lice by currents, and thereby strengthened the connectivity between farms. Additionally, the cluster size may also be influenced by high farm density confined in a smaller area, as observed in cluster 23. PZ6 also encompassed moderately sized clusters which were located in fjords. Conversely, the

infestation networks of PZ4 and PZ5 had averagely smaller clusters than clusters in PZ6. Generally, the cluster size varied depending on factors such as fjord size, the number of farms, and the extent of coastline covered by the farms. In PZ4, there were variability between smaller clusters and larger clusters. This may be attributed to the farm´s geographical locations in fjords and coastlines. Within fjords, the clusters emerged smaller or larger depending on the number of farms present, as observed in cluster 5 and cluster 45 in PZ4. The false clusters were farms that were not assigned to any cluster and showed zero lice infestations. The false clusters had low connectivity to other farms, and thereby was not divided into a cluster by the model.

Larger clusters containing more farms may require more extensive collaboration of management compared to smaller clusters. However, larger clusters have proven the most effective in reducing connectivity between internal farms within clusters (Adams et al., 2016). Studies have shown that connectivity between internal farms decreases as the size of management units increases, and the probability of external infestation is lower in larger units (Adams et al., 2016). Nevertheless, smaller management units are also beneficial and can reduce 75% of external infestations by coordinated efforts compared to individual farms (Adams et al., 2016). All three PZs thus have the potential to benefit from synchronized production. The efficacy of treatment and fallowing periods are more effective if they are coordinated among farms that are connected. Coordinated fallowing may result in reduced infestation pressure from the previous production cycle and surrounding sites when restocking (Stige et al., 2024).

4.2 - Methodology

The bio-physic dispersal model simulated lice dispersal based of ocean currents and historical production data, which was implemented with time and the spatial arrangement of farms across the four-year study period. Hydrodynamic models have been widely used in studies to provide valuable insights and knowledge on lice connectivity in Norway (Huserbråten et al., 2020a, 2020b; Huserbråten and Johnsen, 2022; Samsing et al., 2017; Sandvik et al., 2020), Scotland (Adams et al., 2012; Murray and Gillibrand, 2006; Salama et al., 2018; Scanlon et al., 2021), and Canada (M. G. G. Foreman et al., 2015). Using models to simulate lice dispersal enables full-scale experiments and analyses of the infestation network that would not be feasible in practise. The models provide opportunities that would otherwise be too expensive or impossible

to study scientifically. The method used to simulate lice dispersal and connectivity between farms provide valuable insights of the infestation network structure.

However, it is important to note that the infestation networks are only simulations and theoretically representations of the actual network. The model calculated the lice dispersal between farms on an hourly basis across the study period. Potential lice infestation occurs only if the receiving farms produce fish at the same time as infestation exists between farms. The network presented is the average representation of infestation across the four-year study period, where release of lice and the timing of fish at the farms can affect the average results. Moreover, the lice dispersal is calculated based of the number of fish, temperature and the number of lice reported weekly at each farm by the farmers. However, uncertainties remain regarding the accuracy of the lice counting and whether samples of 20 fish are representative for the actual lice release at the farms (Heuch et al., 2011).

A limitation of the method could also be the exclusion of salmon lice infestation originating from wild salmonids. The presence of wild salmonids may vary seasonally, and occasional high numbers of wild salmonids could impact the infestation pressure at farms. However, studies have demonstrated that 99.1% of adult female salmon lice originate from farmed salmonids (Dempster et al., 2021). The connectivity here is thus representative, but the farms can also experience additional lice infestations which is not considered here.

The hydrodynamic modelling represents current and circulation conditions well compared to actual scenarios. However, some episodic deviations have been documented between modelled and observed currents, where the current model performed well in 87% of the time in observations from 2017, and 64% of the time in 2016 (Dalsøren et al., 2020). The model have demonstrated good validation of salinity and temperature, with only 1°C and one unit difference in observations (Asplin et al., 2020).

Model performance has improved over the years as lice parameters have been implemented according to updated research on lice biology from laboratory experiments (Crosbie et al., 2019; Sandvik et al., 2020). The models are however not only used to analyse lice infestations between farms, but also to assess environmental conditions, specifically lice infestation on wild salmonid populations (Johnsen et al., 2021; Karlsen et al., 2023; Qviller et al., 2024; Vollset et al., 2023a, 2023b, 2022), to assess sustainability (Sandvik et al., 2021a), and climate change effects

(Sandvik et al., 2021b). Simulations of the development of treatment resistant lice has also been performed (Coates et al., 2022). As these models are increasingly used in research as a recognized method, they are being refined to become more accurate and reliable, thereby creating even more realistic representations of lice dispersal and connectivity.

4.3 - Connectivity Patterns

The connectivity infestation networks showed spatial variations in lice infestation pressure between farms throughout the study area. The infestation network of PZ5 showed reduced connectivity, where a lower number of lice was transferring between the farms compared to the number of lice transferring between farms in PZ4 and PZ6. One possible explanation for the reduced connectivity can be the lower biomass of salmonids produced in PZ5, resulting in a lower infestation pressure.

Farms with the highest infestation pressure within clusters were primarily located in the fjords in PZ5 and PZ4, where the strongest connections also were observed. However, the infestation pressure in PZ6 seemed to be more consistent in lice pressure at farms, with strong connections observed between farms in both fjords and open coastal areas. The different connectivity and infestation patterns may be explained by the farm´s geographical locations where varying levels of lice are typically present. Studies have shown that farms located in open coastal areas are exposed to a lower lice concentration than farms located within fjords (Johnsen et al., 2016). The lice concentration is more diluted by a larger geographical area in open coastal areas, in contrast to within fjords, which cover a smaller geographical area, contributing to a higher lice concentration (Johnsen et al., 2016). The higher lice concentration in fjords does not necessarily mean higher lice infestation pressure, as infestation pressure is dependent on lice transmission between the farms. However, this dilution effect could explain why higher infestation was observed in clusters located in fjords compared to coastal areas in PZ5 and PZ4.

Connectivity was created when water exchanged between farms and where production of fish and lice infestation occurred at the same time. Connectivity in the model is dependent on the release of lice, current circulation, the farms´ geographical locations and the presence of fish. Identifying the primary factor driving variability in lice connectivity is difficult, as the model do not specify this.

The transmission of lice had the longest dispersal distances in PZ6, where minimal long-distance lice dispersal was observed in PZ4, and shorter lice dispersal distances in PZ5 than in PZ6. This pattern corresponds to the distribution of farms in open coastal areas in PZ6, and some areas in PZ4, potentially giving larger dispersal distances influenced by the ocean currents. Conversely, farms located within fjords typically displayed shorter lice dispersal ranges.

The connectivity patterns within fjords revealed both inward and outward movements of lice. This is a result of the general circulation within fjords, where water current alternate between flowing outward and pulsating inward (Asplin et al., 2014; Johnsen et al., 2016). Wind forces may also influence connectivity patterns (Adams et al., 2012). This connectivity pattern contributed to strengthening the connectivity between farms within the fjords, thereby additionally explaining the higher connectivity observed within fjords compared to open coastlines in PZ5 and PZ4.

The lice dispersed predominantly in a northern direction in open coastlines across all three PZs. The northern direction of lice dispersal reflects that lice larvae are transported northward by the coastal current that runs from south to north along the coast (Sætre, 2007) (Figure 2.4). One exception was observed in cluster 17 in PZ6, where lice had a southern dispersal drift. The southern dispersal drift may be explained by episodes of high infestation pressure at certain times that have dominated the average infestation picture calculated by the model. The northern wind is stronger during the summer, which may have dispersed the lice southwards (Gade, 1986). During the summer, the farms may also have housed larger fish, which may have increased the infestation pressure, as larger fish exhibit more lice (Tucker et al., 2002). As a potential result, a higher number of lice dispersed, thereby creating connectivity to southern located farms.

4.4 - Total Infestation Pressure

Each production zone exhibited prominent clusters with higher total lice infestations. Cluster 5 in PZ4 had the highest infestation pressure of all three PZs. Cluster 2 in PZ6 and cluster 25 in PZ5 also displayed higher infestation pressures. However, the high infestation pressure could also reflect the large number of farms present in cluster 5 and 2, which were the largest clusters in size. Nevertheless, the clusters are here highlighted, indicating that measures to reduce lice

infestations could be beneficial for both farmers and to reduce impact on wild salmonid populations.

When examining the average infestation pressure per farm, the highest number was shown in PZ5. The significant positive correlation between the number of farms and total lice infestation of all PZ in Norway indicates that reducing the number of farms may be a solution to lower total lice infestation levels in each PZ. However, the amount of unexplained variance in the regression model was moderate, indicating existence of other factors.

PZ6 had the lowest infestation pressure per biomass (Table 3.2), despite having the highest production intensity across all three PZs (Table 2.1). One reason for this may be the colder water temperature in PZ6 than for PZ4 and the southern parts of PZ5 (Figure 2.3). The growth rate of salmon lice is temperature dependent and develop faster as temperature increases (Hamre et al., 2019; Samsing et al., 2016b). Additionally, higher biomass doesn't necessarily give higher infestation. On the contrary, studies have shown a negative relationship between biomass and lice infestations due to the dilution effect (Samsing et al., 2014; Van Walraven et al., 2021). Additionally, the biomass may have been distributed more optimally in PZ6 during the study period, where larger farms that produced higher biomass of fish were located in open coastal areas where lice concentration generally is lower (Johnsen et al., 2016). Higher biomass on larger farms with greater distance between them have shown to be an effective preventative measure against salmon lice infestations (Qviller et al., 2024). This optimal management strategy and the lower water temperature may have contributed to a lower infestation pressure in PZ6 although the biomass produced was high.

The lice infestation pressure per biomass may also reflect each PZ´s traffic light colour. The traffic light colours are generally assessed based of lice induced mortality on wild migrating salmon smolt in each production zone. Green colour are assigned to production zones exhibiting lower lice infestations which result in lower impact on wild populations. PZ6 had the lowest infestation pressure per biomass, and was also assessed to have low infestation and low impact on the wild populations. PZ4 and PZ5 had respectively higher infestation per biomass, which may reflect the red and yellow traffic light colours, indicating higher impact on wild populations.

The total infestation was defined based on total lice import. However, the same results would have been made if lice export was selected, as there was a strong significant positive correlation

between lice import and export. The correlation implies that farms imported a similar number of lice as the farms exported. The correlation offers predictability, allowing to infer lice export levels by monitoring lice import. This may suggest that if we were to reduce the number of lice imported, the number of lice exported could also be reduced. Decreased lice infestation imported and exported will not only lower the overall lice levels at individual farms, but also within clusters, as the lice export to nearby farms will decrease. This emphasize the importance of coordinated management strategies within clusters. Conversely, an increase in lice import would lead to a rise in lice export, thereby affecting adjacent farms and strengthening the connectivity between them. This is a contrast to previous studies that has indicated that management at high connectivity influx was likely to offer the most cost-effective reduction in lice numbers (Adams et al., 2015). Here, we have demonstrated that managing farms with high lice import or export may give the same effect.

4.5 - Isolation

The emerged clusters were in general highly isolated across all three PZs, with some spatial variations within the networks. The clusters´ isolation ratios reflect the percentage of internally sourced lice infestations. A high isolation ratio indicates low external influence, and a low isolation ratio indicates high external influence. Overall, the clusters showed a high amount of internal infestation, with low external infestation. The highly isolated clusters implies that the clusters can be effectively utilized for coordinated management, as there is strong connection among the farms within each cluster, and relatively little infestation from external farms. Coordinated management could involve synchronizing farm operations such as lice treatments, fallowing periods, stocking, and harvesting within clusters to optimally reduce lice infestations and re-infestations from connected farms. Moreover, highly isolated clusters could also be the result of already implemented coordinated efforts between the farms in the study area, as our network analysis is based on historical data of biomass and the release of lice at the farms.

Some clusters with relatively high isolation ratios were located within fjords, as observed in cluster 20, 25 and 22. However, some clusters with low isolation were also located within fjords, such as cluster 36 in PZ6 and cluster 56 and 45 in PZ4. This indicates that the isolation ratios may not be correlated with the location of clusters within fjords. However, the alternation of water flowing outwards and pulsating inwards within fjords (Asplin et al., 2014; Johnsen et al., 2016), can create stronger connectivity between internal farms, potentially resulting in higher

isolation. Isolated clusters within fjords seems reasonable as the fjords naturally segregate internal farms from external farms. However, the isolation may be further influenced by barriers or internal farms located in the fjord entrance with close proximity to external farms, making them more susceptible to external infestation. This could create variability in isolation between clusters located within fjords.

Clusters located at open coast are more influenced by the north directed coast current (Sætre, 2007) than clusters located within fjords. However, only in cluster 15 this seemed to have an influence on the isolation ratio. Cluster 15 had relatively lower isolation, which may be explained by its extensive coverage of the coastline, and the higher coast current speed observed in this area (Figure 2.4). The lice dispersed over larger distances, infecting farms far away and farms outside the cluster. Cluster 15 also received infestation from farms in production zone 3, which was discovered during the network analysis. The northern movement of lice seemed to have an impact on this cluster´s isolation, but this was not observed in other coastline located clusters where the coast current speed was generally lower (Figure 2.4).

Some clusters demonstrated both relatively high isolation ratios and high total infestation pressures. The higher isolation ratios indicate that the high infestation pressure observed in these clusters were internally sourced, with a small proportion of external infestation. The infestation pressure and isolation thus do not mean the same. High isolation and high total infestation may be explained by large cluster size, where infestation remains between internal farms due to the cluster is covering extensive areas, as observed in cluster 2. A reason could also be the absence of external farms near the clusters. High connectivity between internal farms can also explain why infestation remains between internal farms within the cluster, as seen in cluster 25 and 5. Large clusters have a lower probability of external infestation, which is reflected in cluster 5 and 2 (Adams et al., 2016), but the internal infestation can still be high, thus the infestation pressure remains high.

The individual farms were in general less isolated compared to the clusters. This difference between cluster isolation and farm isolation highlights the potential efficacy of coordinated management efforts over individual farm management. The strong connectivity between farms plays a smaller role when examining the infestation network from a cluster perspective. An additional observation is the variability in isolation ratios among farms within clusters. The infestation networks revealed that farms with the lowest isolation were located at the coast,

whereas the farms with higher isolation were located in the fjords. This seems reasonable as the coastal current is more unidirectional at the coast than in fjords (Sætre, 2007), and thus lice can disperse more easily over larger distances. The lice tend to accumulate in areas close to shore, and in narrow areas and bays, which can further explain the higher isolation within fjords (Asplin et al., 2014). The positive significant correlation between farm isolation and the distance to open sea supports this statement. The farm isolation ratio increased further inward the fjords the farms were located, and decreased in open coastal areas. This shows that the farms located within fjords had higher internal infestation relative to external infestation compared to farms located in open coastal areas. However, there was also a high proportion of unexplained variance, suggesting that additional factors may influence this observed pattern. These factors could for instance be the natural variability in current flow and wind forces, where local variations could create differences in isolation. The distance between surrounding farms may also be a factor here.

The lice larvae moved from less isolated farms located in open coastlines and dispersed inward to farms within the fjords. This pattern of lice dispersal has been observed in examination of lice resistance across the Norwegian coast (Coates et al., 2022). The dispersal of treatment resistant lice was simulated, revealing a pattern of resistant lice evolving on the west coast, moving inward the fjords. The coast is strongly coupled with the coast current, thereby dispersing the resistant lice northward by time (Coates et al., 2022). This could potentially mean that less isolated farms, can transmit infestation inward to the fjords more easily than if they were more isolated. Regions of high farm connectivity was potential hotspots of louse adaptation (Coates et al., 2022). By increasingly isolating clusters of farms and synchronising lice preventative operations, the connectivity between internal farms could be decreased (Adams et al., 2016), which could slow down the dispersal of resistant lice.

Another point is that the clusters in the network may not be optimally aligned with ocean currents, as they are also influenced by production cycle data in the modelling. The farms may have been grouped differently into clusters if ocean currents were the only factor considered in the model. In that case, the farms in each cluster would have produced the same number of lice, and the variation in cluster infestation pressure would have been eliminated. The connectivity between farms and the isolation ratios would then be influenced more by geographical and oceanographic factors rather than differences in lice infestation pressure. Clusters located in areas with slower current speed, might become more isolated, since the lice would have not

drifted over long distances. Conversely, clusters located along open coastlines, with stronger current northwards, would likely experience decreased isolation. The strong currents would facilitate the dispersal of lice between farms in different clusters, thereby increasing the external infestation and reducing the cluster isolation. Additionally, different external infestation sources could have been identified, as the coast current moves northwards. Moreover, natural geographical barriers such as peninsulas, islands or inlets could play a more significant role in determining clusters and their isolations. Barriers could prevent lice flow between clusters, thereby increasing the cluster isolation. The mentioned scenario would be interesting to explore in future research. Nevertheless, the infestation networks generated in this study, provide a realistic representation of the historical lice infestation network, which remains relevant today.

4.6 - Isolation Versus Infestation Pressure

The use of hydrodynamic models opens opportunities for further research on infestation networks, which otherwise would be challenging, costly or impractical to investigate in practice. Testing various lice control measures can be done by virtually remove farms to examine the effect on different factors (Qviller et al., 2024; Samsing et al., 2019). While not providing a perfect representation, these models can guide management in the right direction. Here, we tested if removing farms could create even more isolated clusters in the networks.

The number of external infestation sources and recipients varied between clusters, resulting in different effects on isolation when external farms were removed. The results showed that the isolation ratio increased rapidly for clusters with few external infestation sources compared to clusters with multiple farms contribution to external infestations. Additionally, the total cluster infestation decreased for all clusters when removing external farms from the infestation network. The clusters with highest initial isolation showed a smaller reduction in total infestation compared to clusters with lower initial isolation. The results suggest that targeting clusters with lower isolation and fewer external infestation sources is optimal when removing external farms to reduce total infestation pressure and increase cluster isolation. The effect of removing farms could be practically achieved in salmon farming by either physically remove farms, relocate farm or biomass, fallowing farms, or change technology from open to closed confinement systems (A. Nilsen et al., 2017; Qviller et al., 2024). Using preventative methods such as barrier technology like skirt and snorkels could also create the same effect (Oppedal et al., 2017), but probably not as efficient as closing or removing the farms. Only external farms were removed

in this analysis, however internal farms could also be virtually removed using hydrodynamic models. The effect of removing both external and internal farms could be of interest for future research on isolation.

Before the analysis, it was likely that the clusters would be isolated, as the model were designed to create clusters where lice dispersal was higher within then between clusters, by calculating community structures (Huserbråten et al., 2020a). However, this network analysis confirmed that the clusters were in fact isolated and may be useful for the salmon farming industry. Even though the clusters emerged isolated, the results also demonstrated that further isolating the clusters is possible. Nevertheless, completely isolated clusters across the entire infestation network, would be a practically impossible task. Lice can drift over long distances with the ocean currents, depending on their survival time in the pelagic phase, and seasonal temperature variations where the dispersal distance increase in cooler temperatures (Huserbråten and Johnsen, 2022; Samsing et al., 2017). The dispersal distances may also be enhanced by occasional large scale wind forcing events (Huserbråten and Johnsen, 2022). The actual travel distance for copepodids is generally between 20-40 km away from the source, and few can drift up to 100 km (Asplin et al., 2014). Thus, lice have the potential to affect farms located far away. Consequently, there are inherent limitations on how isolated clusters can become, as it is impossible to control the drift duration of lice.

An effective lice management strategy could involve coordination of smaller production units, like the clusters provide, using an integrated pest management approach (Sommerville, 1998). Synchronizing fallowing and treatment periods can ensure that the production cycle starts producing fish with the lowest number of lice as possible, while at the same time preventing re-infestations from adjacent farms to occur. This approach could lead to reduced treatment requirements (Murray and Salama, 2016), which is advantageous for reducing production loss and improving fish welfare (Overton et al., 2018). By identifying isolated clusters we can ensure that the effect of coordinated efforts, such as fallowing and lice treatments, have optimal effects due to low external infestations. Additionally, by identifying farms with high or low infestation pressures within clusters, we can pinpoint farms that would benefit from targeted measures to reduce infestations. Within clusters, biomass could be allocated from areas with high lice pressure to areas with low lice pressure (Qviller et al., 2024). Other measures could be to stock with larger fish to reduce the lice exposure time in areas that often show high lice numbers, or remove farms from the infestation network to benefit the rest of the farms within the cluster

(Stige et al., 2024). Ultimately, this can result in lower lice infestations, which at the end could reduce the environmental impacts on wild salmonid populations. Small differences in management practices have the potential to facilitate substantial gains in a long-term perspective.

The term isolation is valuable in assessing the potential efficacy of coordinated management measures aimed at reducing total lice infestations. The isolation doesn't directly reflect the lice infestation pressure in an area, since highly isolated clusters can still experience high infestation pressure due to high internal infestations. However, the isolation describes the proportion of the infestation that is sourced from internal farms versus external farms. Conversely, the isolation can also indicate areas where measures will have zero local impact, allowing us to avoid implementing extensive interventions in low isolated areas that will not be effective when infestation originates externally. It serves as a practical measure when assessing the impact of local coordinated efforts. One industry goal could be to systematically reduce infestations cluster-wise, which may be achievable since the emergent clusters were in fact highly isolated.

Nevertheless, isolation is not a perfect measure on its own, and should be considered in conjunction with the total infestation pressure. The total infestation pressure provides a concrete number, reflecting the overall lice situation and potential environmental impacts. Measures that reduce the total infestations and increase the isolation ratio would be a good strategy, for instance by strategically removing specific farms that contribute to external infestation.

For future research, exploring the partitioning of farms into clusters based solely on ocean currents, in a scenario where each farm produces the same number of lice, would be interesting. This approach could provide insights into the significance of lice dispersal via ocean currents, and its effect on the cluster isolation. Additionally, investigating the potential effects of removing both internal and external farms to enhance cluster isolation could be valuable, especially for clusters that exhibit few infestation recipients.

A spatiotemporal management approach, supplemented with other preventative methods, may provide an optimal solution for handling salmon lice. The need for costly delousing treatments may decrease in the future, as preventative methods are increasingly utilized (Barrett et al., 2020; Nilsen et al., 2020). This study demonstrated that using bio-physical dispersal models could serve as a prophylactic measure against salmon lice by identifying highly isolated clusters,

that can facilitate coordinated management practices such as synchronized fallowing and treatment periods, aimed at reducing lice infestations. This methodology could provide valuable insights and knowledge that can facilitate industry growth without increasing lice infestations, resulting in a more sustainable salmon farming.

5 Conclusion

A network analysis was performed on lice infestations and connectivity between farms in three production zones in Norwegian salmon farming. A bio-physical dispersal model was used to simulate lice dispersal and calculate connectivity between farms. The methodology enables analyses of infestation networks which would not be easy by other approaches and is a recognized method in the scientific community.

In study aim *(i),* we mapped the infestation networks in PZ6, PZ5 and PZ4, that were fragmented into clusters. Generally, the clusters emerged within fjords and open coastlines, where the cluster size varied depending on fjord size, the number of farms, and the extent of coastline covered by the farms. The network analysis revealed spatial variations in lice infestations and connectivity between farms and clusters of farms. The lice dispersed predominantly in a northern direction in open coastlines across all three PZs. There were highest number of strong connections between farms in PZ4 and PZ6. Farms located within fjords had in general higher infestation than farms located at open coastal areas within PZ4 and PZ5, but there was no such pattern in PZ6. Additionally, a strong positive correlation was detected between lice import and lice export at farms across all 13 PZs in Norway.

Study aim *(ii)* revealed that the clusters were highly isolated, with high internal infestations and low external infestations. Highly isolated clusters may indicate that coordinated management practises within clusters could be an effective approach to reduce lice infestations, by for instance synchronizing treatment or fallowing periods. The individual farms were in general less isolated compared to the clusters. The individual farm isolations varied within clusters, but was higher in fjords than in open coastal areas.

Study aim *(iii)* showed that the clusters had a variable number of external infestation contributors. The clusters achieved a higher isolation ratio and a lower infestation pressure when external farms were removed strategically from the infestation networks. The clusters

with lower isolation ratios and fewer external infestation sources had greatest increase in isolation, and greatest decrease in infestation pressure when removing external farms. Isolation may be a good term to describe the efficacy of coordinated management efforts. The term however should be seen in conjunction with the total infestation pressure.

This study demonstrates that using bio-physical dispersal models can provide information that can be used to prevent and reduce lice infestations. Here, we have identified highly isolated clusters that could represent potential alliances to collectively reduce lice infestations.

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7 Appendix

7.1 - Appendix A

Correlation plot of lice import and lice export across all farms in Norway (Figure 7.1).

Correlation plot of external and internal infestation across all farms in Norway (Figure 7.2).
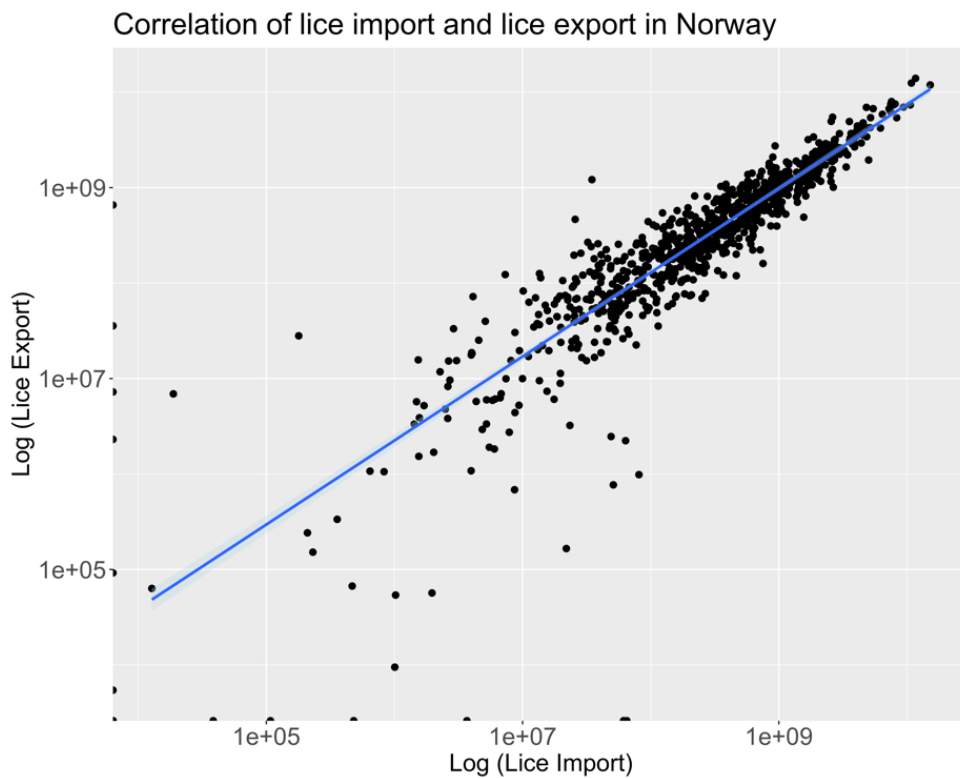

Figure 7.1: Scatter plot showing the correlation between lice import and lice export across all production zones in Norway. The logarithmic scale is applied for both axes to clearly illustrate the data distribution. The linear model (-1.288 + 1.018e+07x = y) demonstrated a strong positive correlation with a p-value<0.001, and R^2 value of 0.9107. The plot indicates that higher lice import is associated with higher lice export.

Correlation of external and internal infestation in Norway
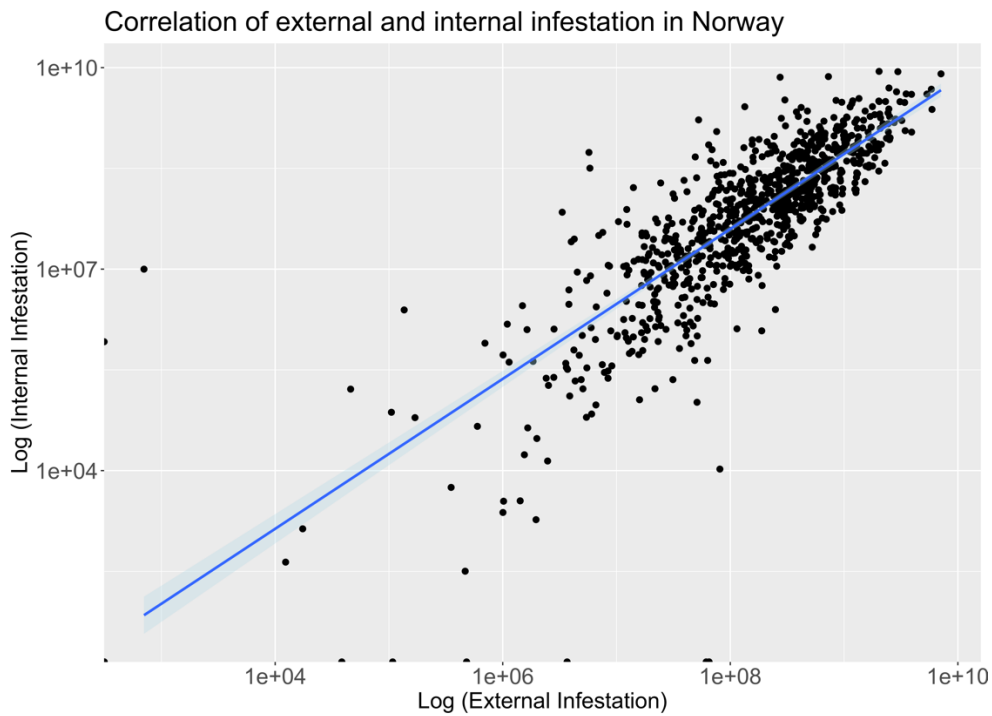
Figure 7.2: Scatter plot illustrating the correlation between internal lice infestations and external lice infestations at farms across all PZs in Norway. The logarithmic scale is applied for the x-axis and y-axis. The linear model (2.017 + 5.5416e+07x = y) showed a positive correlation with a p-value <0.001, and R^2 value of 0.4485, suggesting that high internal lice infestation is associated with high external lice infestations.

7.2 - Appendix B

Isolation ratios of each cluster in each PZ in the study area.

Table 7.1: Isolation ratios of each cluster in PZ6

Cluster	Isolation ratio
22	0.986
2	0.939
23	0.921
17	0.912
36	0.827

Table 7.2: Isolation ratios of each cluster in PZ5.

Cluster	Isolation ratio
25	0.995
41	0.986
12	0.962

Table 7.3: Isolation ratios of each cluster in PZ4

Cluster	Isolation ratio
20	0.986
14	0.956
5	0.955
16	0.928
61	0.919
45	0.900
54	0.890
15	0.872
56	0.824

7.3 - Appendix C

Infestation networks with cluster isolation ratio and farm isolation ratio in each PZ of the study area.
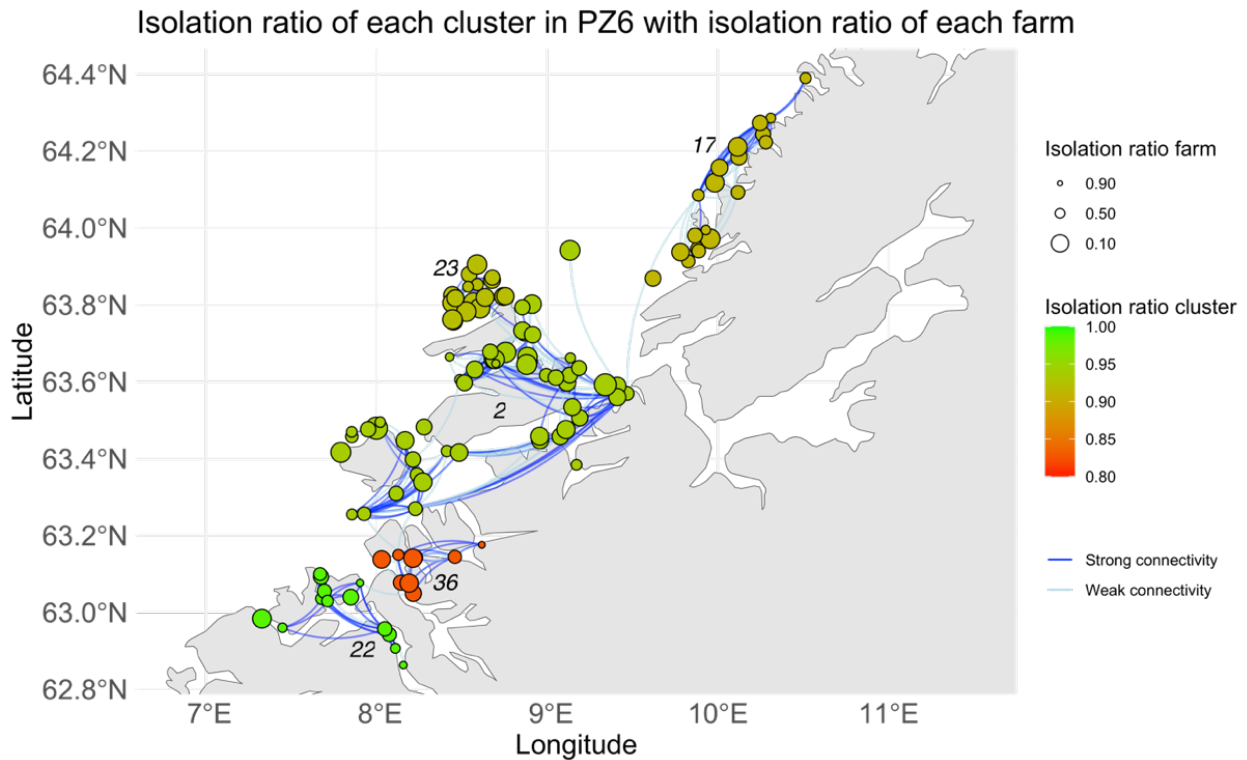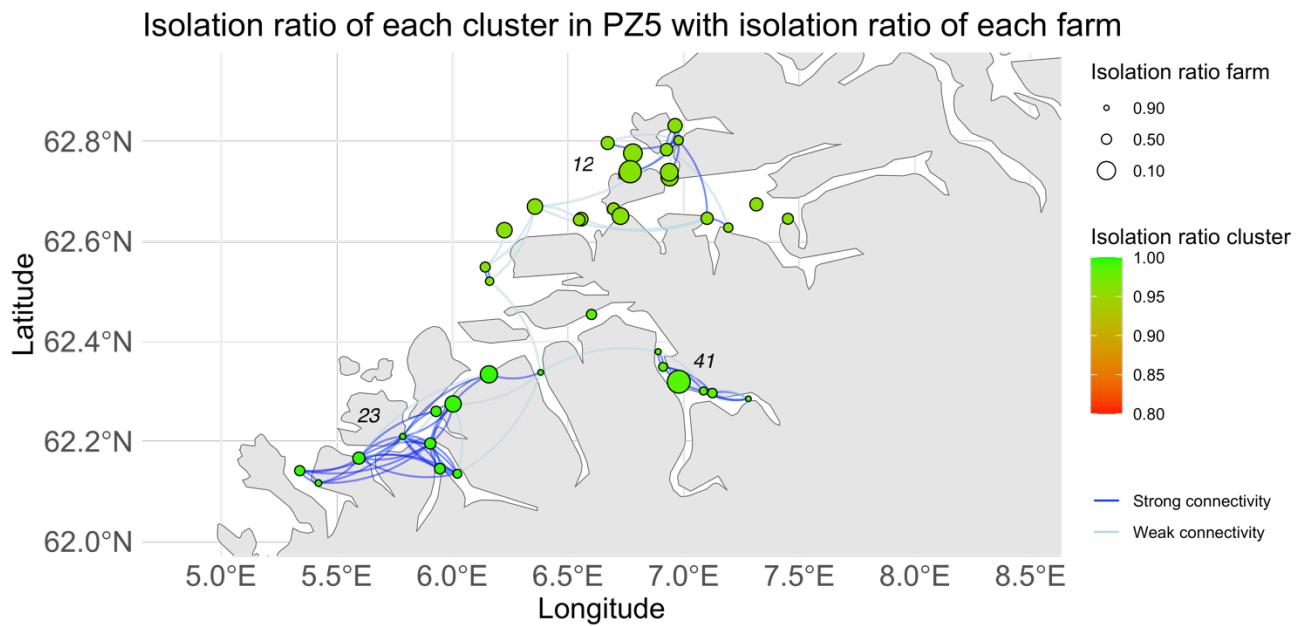

Figure 7.3: The infestation network of PZ4 presenting the isolation ratio of each cluster, and the individual isolation ratio of each farm, and the connectivity between them. Circles represent individual farms located in the clusters. The small numbers represent the cluster number. The circle size is scaled according to lice import, reflecting each farm´s individual infestation pressure. The colours represent the isolation ratio of each cluster, where the colours are scaling from green to red, reflecting low to high isolation. Connectivity between farms are represented with arced blue lines where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice.
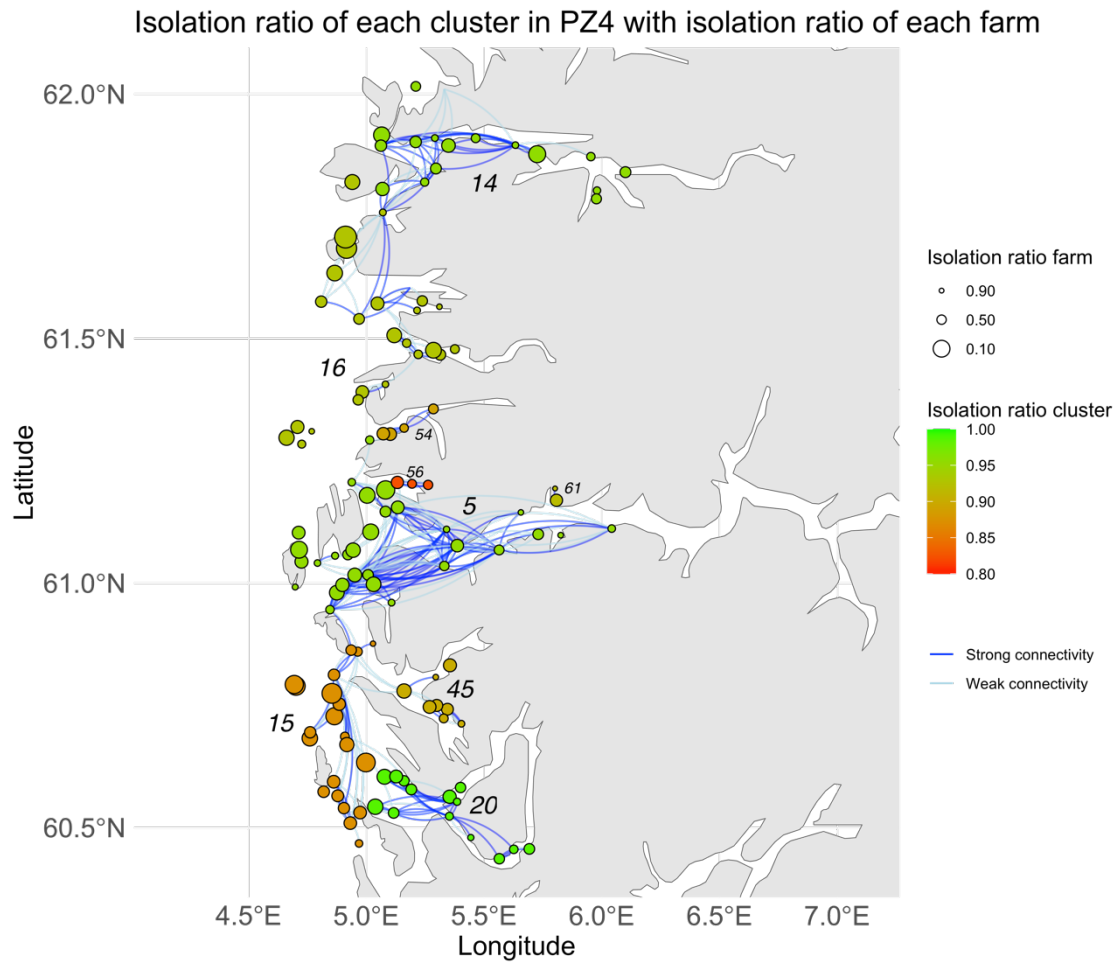
Figure 7.4: The infestation network of PZ5 presenting the isolation ratio of each cluster, and the individual isolation ratio of each farm, and the connectivity between them. Circles represent individual farms located in the clusters. The small numbers represent the cluster number. The circle size is scaled according to lice import, reflecting each farm´s individual infestation pressure. The colours represent the isolation ratio of each cluster, where the colours are scaling from green to red, reflecting low to high isolation. Connectivity between farms are represented with arced blue lines where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice.

Figure 7.5: The infestation network of PZ4 presenting the isolation ratio of each cluster, and the individual isolation ratio of each farm, and the connectivity between them. Circles represent individual farms located in the clusters. The small numbers represent the cluster number. The circle size is scaled according to lice import, reflecting each farm´s individual infestation pressure. The colours represent the isolation ratio of each cluster, where the colours are scaling from green to red, reflecting low to high isolation. Connectivity between farms are represented with arced blue lines where lice move in a counter-clockwise direction. The lines do not reflect the actual drift route taken by the lice.

7.4 - Appendix D

External infestation sources and recipients in bar charts and maps for cluster 5, 12, 23, 2 and 45 in PZ4, PZ5 and PZ6. In these maps, the top 50 connectivity lines were illustrated, where the 30 strongest were defined as strong, and the following 20 as weak.

Cluster 5
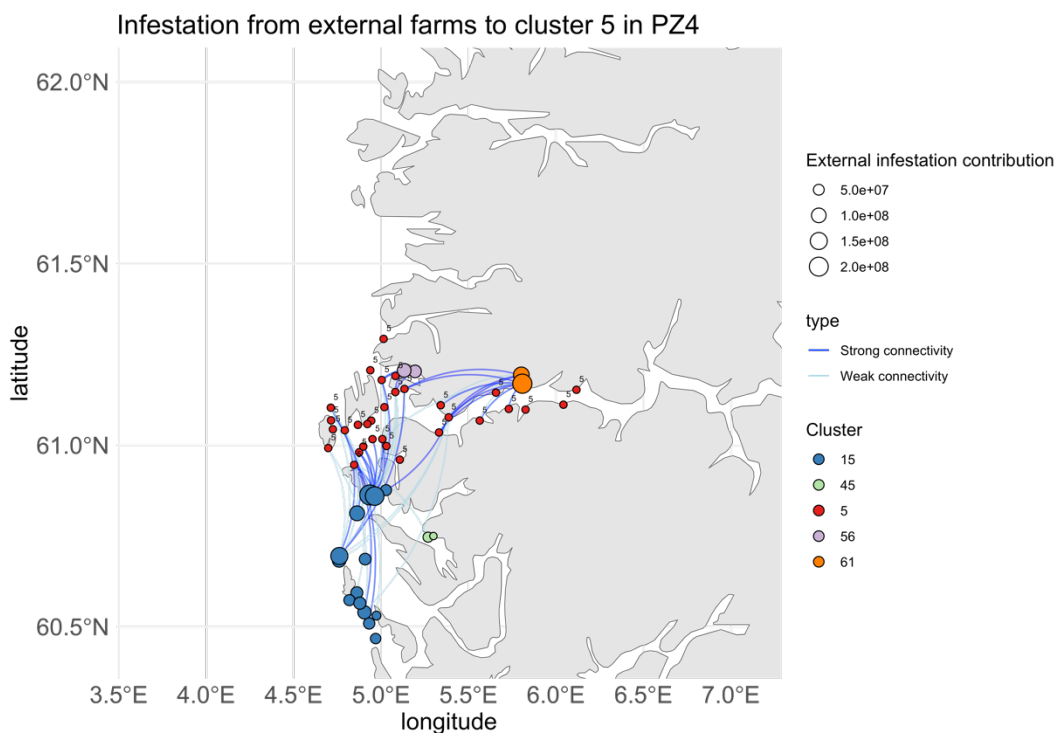
Figure 7.6: Cluster 5 and its external infestation sources with connectivity between external and internal farms. Circles represent external and internal farms. The colours are scaled according to cluster affiliation where red colour represent cluster 5. The circle size is scaled according to the number of lice transferring to the cluster from external farms. Connectivity between external and internal farms are represented with arced blue lines, where lice move in a counter-clockwise direction. Top 50 connectivity lines are illustrated. The lines do not reflect the actual drift route taken by the lice.
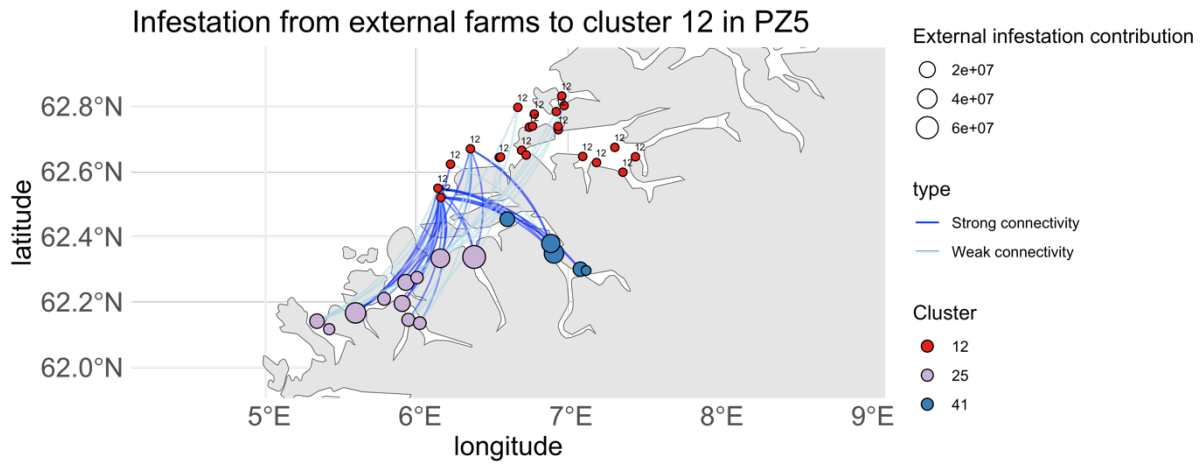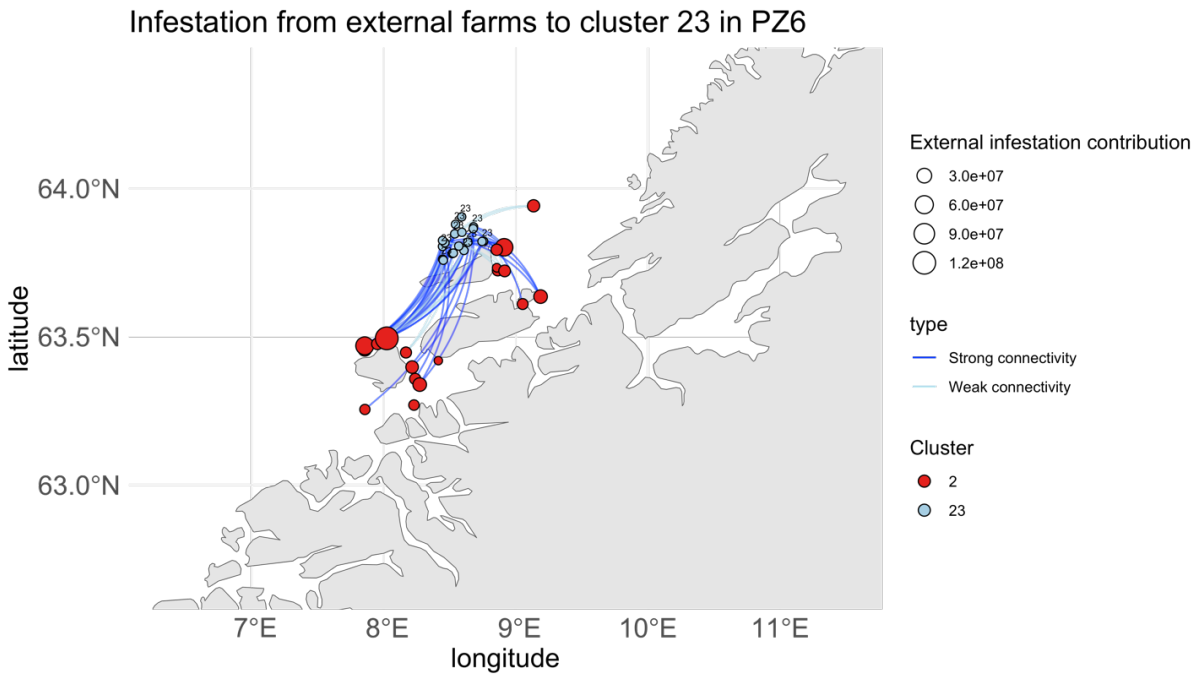
Cluster 12

Figure 7.7: Cluster 12 and its external infestation sources with connectivity between external and internal farms. Circles represent external and internal farms. The colours are scaled according to cluster affiliation where red colour represent cluster 12. The circle size is scaled according to the number of lice transferring to the cluster from external farms. Connectivity between external and internal farms are represented with arced blue lines, where lice move in a counter-clockwise direction. Top 50 connectivity lines are illustrated. The lines do not reflect the actual drift route taken by the lice.

Cluster 23

Figure 7.8: Cluster 2 and its external infestation sources with connectivity between external and internal farms. Circles represent external and internal farms. The colours are scaled according to cluster affiliation where red colour represent cluster 2. The circle size is scaled according to the number of lice transferring to the cluster from external farms. Connectivity between external and internal farms are represented with arced blue lines, where lice move in a counter-clockwise direction. Top 50 connectivity lines are illustrated. The lines do not reflect the actual drift route taken by the lice.
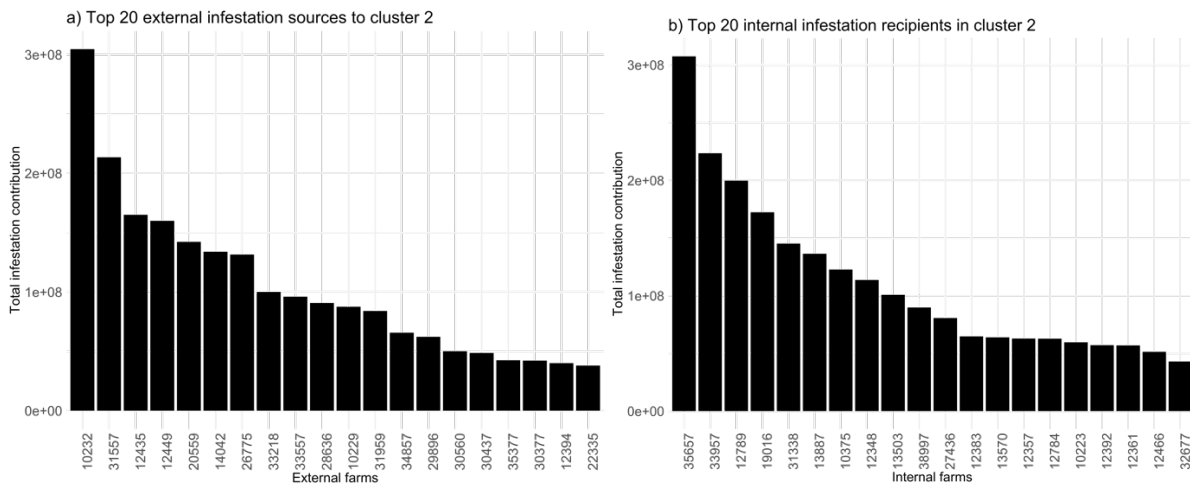
Cluster 2

Figure 7.9: **a)** *Top 20 external infestation sources to cluster 2 in PZ6.* **b)** *Top 20 internal infestation sources to cluster 2. Note that the y-axis is different between the bar charts.*
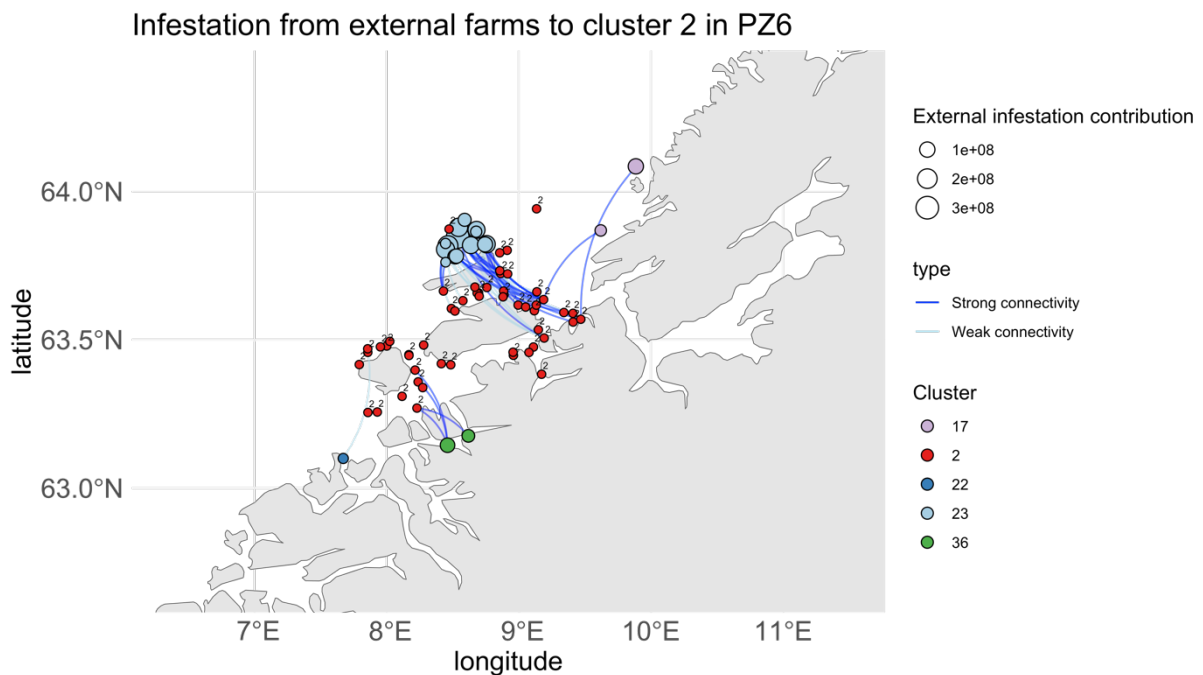

Figure 7.10: Cluster 2 and its external infestation sources with connectivity between external and internal farms. Circles represent external and internal farms. The colours are scaled according to cluster affiliation where red colour represent cluster 2. The circle size is scaled according to the number of lice transferring to the cluster from external farms. Connectivity between external and internal farms are represented with arced blue lines, where lice move in a counter-clockwise direction. Top 50 connectivity lines are illustrated. The lines do not reflect the actual drift route taken by the lice.
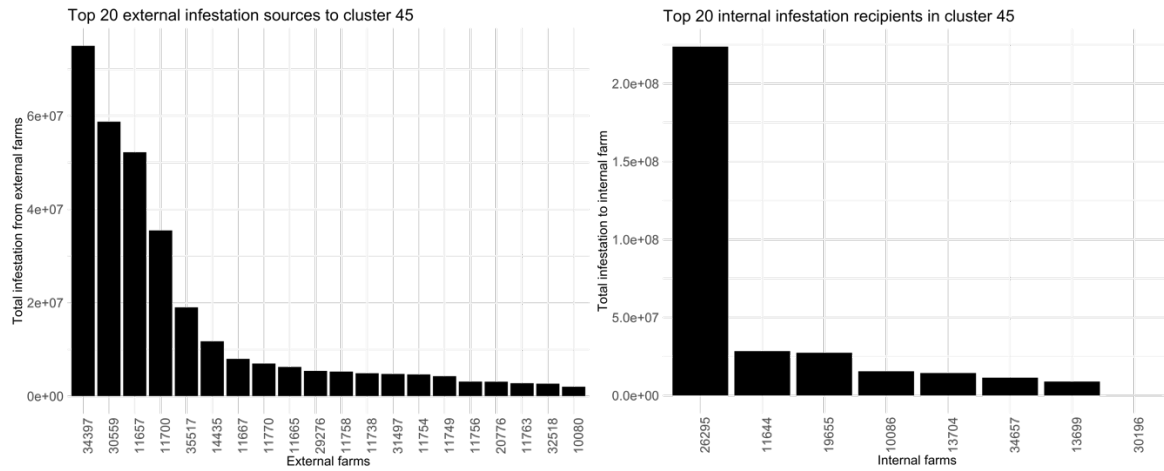
Cluster 45

Figure 7.11: Top 20 external infestation sources to cluster 45 in PZ4 and top 20 internal infestation recipients to cluster 45. Note that the y-axis is different between the bar charts.
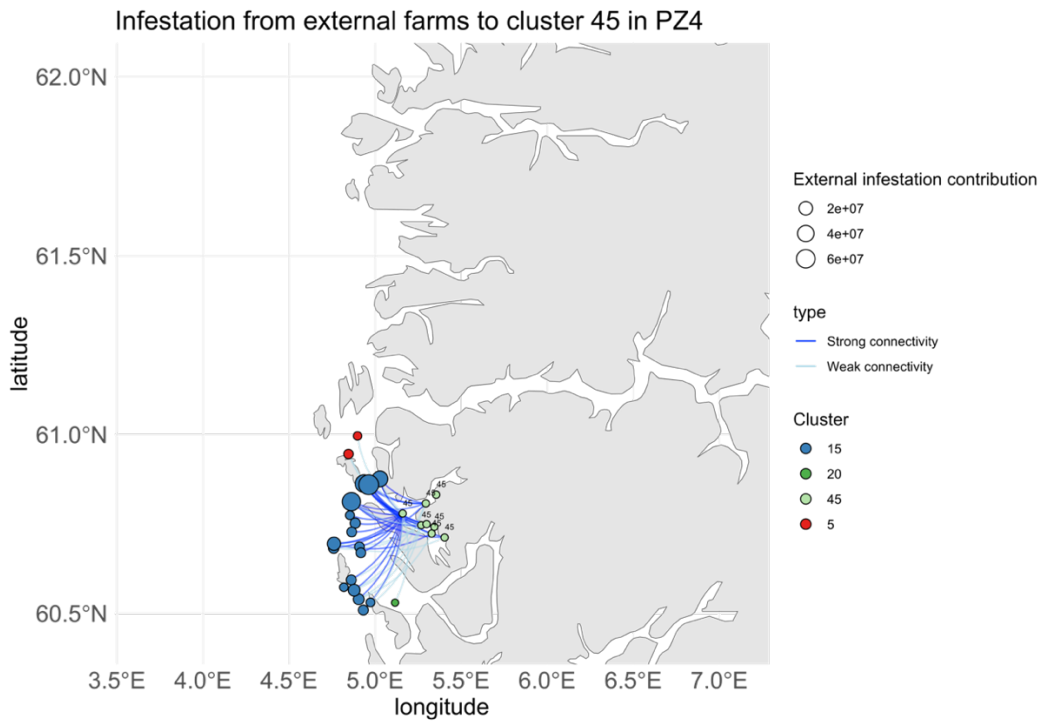

Figure 7.12: Cluster 45 and its external infestation sources with connectivity between external and internal farms. Circles represent external and internal farms. The colours are scaled according to cluster affiliation where red colour represent cluster 2. The circle size is scaled according to the number of lice transferring to the cluster from external farms. Connectivity between external and internal farms are represented with arced blue lines, where lice move in a counter-clockwise direction. Top 50 connectivity lines are illustrated. The lines do not reflect the actual drift route taken by the lice.