## WildFish.

## OPEN NET SALMON FARMING

The impacts of open net salmon farming on wild fish and their environment

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## SUMMARY OF IMPACTS

The complex life cycle of Atlantic salmon has made it historically difficult to gather conclusive evidence about the impact of open net salmon farming on wild populations. However, from very early after the development of aquaculture, trends emerged suggesting that it had a negative impact, not just on wild Atlantic salmon, but on the wider marine ecosystem. As more data has emerged, the evidence has become clearer: salmon farming has a significant negative impact on wild fish and their environment.

At its current scale, the number of Atlantic salmon escaping from farms often exceeds the wild populations they are likely to interact with. Though farmed salmon are physiologically and genetically distinct from wild salmon, causing low survival outside of farms, they compete with wild fish for food, introduce pathogens and increase the rate of predation which reduces wild populations. Farmed escapes also hybridise with wild salmon. Genetic introgression is widespread and significantly associated with proximity to farms. Hybridisation reduces the genetic fitness of individual populations, and the diversity of the whole species.

Even without direct interaction of fish, salmon farming facilitates the transmission of parasitic sea lice from farms into wild populations. The high population density of salmon on farms provides the conditions for acute sea lice infestations, which can be transmitted through the free movement of water into wild fish populations. Atlantic salmon have demonstrably lower rates of survival because of sea lice infection pressure from farms. Sea trout and other salmonids also suffer infections because of salmon aquaculture. Recent attempts to combat sea lice infections in a sustainable manner on farms have focused on the use of cleaner fish that consume lice when stocked in salmon pens, however, serious concerns have emerged around the potential overharvesting of these species from the wild and the poor welfare they experience.

#### SUMMARY

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Alongside sea lice, salmon farms also host many other parasites and pathogens at much higher concentrations than wild populations, which they transmit back into the environment. There is still limited understanding of the causative agents of many salmon diseases, making effective management responses that would prevent transmission into wild populations unlikely. The aquaculture environment has also been demonstrated to facilitate the emergence of novel, more virulent strains of endemic diseases such as infectious salmon anaemia and heart and skeletal muscle inflammation. posing new risks to wild populations.

Salmon farms also emit large amounts of organic waste in the form of uneaten food and faeces. This causes significant reductions in the biodiversity in zones below and around salmon farms on the seabed, and shifts in the community composition, structure and function. The emission of large quantities of chemicals used to treat sea lice also kills or harms considerable marine biodiversity, particularly crustaceans and bivalves, with effects recorded up to 10km away. The use of acoustic deterrent devices to exclude marine mammals that may damage salmon farm equipment also causes harm in many non-target cetaceans.

The biggest impacts of salmon farming on the wider environment, however, are a result of producing feed. Life cycle analysis of salmon farming shows that the production of fishmeal, fish oil, and the highly processed plant protein and fats that are also included, can make up over 90% of the greenhouse gas emissions from salmon farming and have the biggest impact on the sustainability of the harvested salmon.

The scientific evidence available clearly demonstrates salmon farming has significant negative impacts for wild fish across many temporal and spatial scales

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It is an expected and accepted part of the aquaculture industry that farmed salmon frequently escape into the wider environment (Glover et al., 2020). In both freshwater hatcheries and both freshwater and marine open-net pens the farms are dependent on the natural environment to provide a steady flow of well oxygenated water, but this limited separation makes escapes into the wider environment an obvious consequence of any breach. At all stages of growth where salmon are kept in nets there is evidence of both large-scale escape events caused by damage to cages, and the steady release of individuals – known as "drip" escapes – for example by stocking pens with fish small enough to pass through the netting (Wringe et al., 2018; Glover et al., 2017). The official statistics of farmed salmon escapes are considered by scientists to be a significant underestimate, reporting in some instances an estimated 12% of the true volume of escapes.

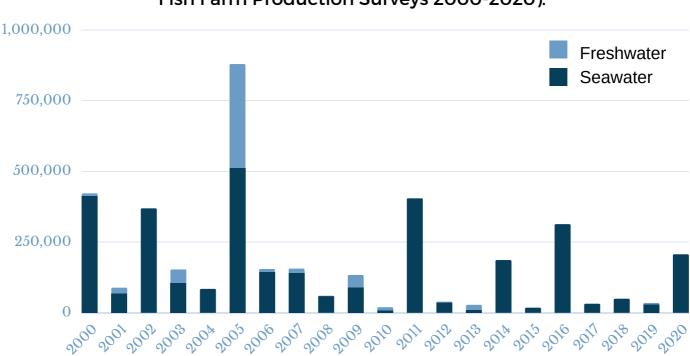
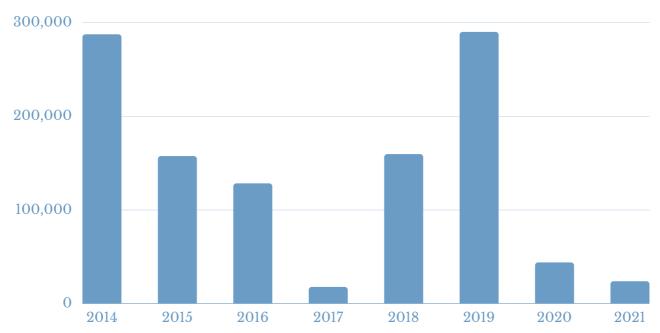


Figure 1. 20 years of escapes reported to the Scottish government (Scottish Fish Farm Production Surveys 2000-2020).

This study found that for a country like Norway, while reported annual numbers may be in the range of 250,000-550,000, the true number of escapes is an estimated 2.4 million, with considerable growth in salmon production since this study was conducted (Thorstad et al., 2008). Records of the number of escapes from salmon farms across Scotland and Norway demonstrate the regularity and scale of these events (figure 1-2). Planned expansion of marine aquaculture from 200,000 tonnes of salmon produced in 2020 to 300,000 tonnes in 2030 is dependent on building capacity outside of sea lochs and voes on the continental shelf (Tett et al., 2018). As salmon aquaculture expands into new, less sheltered areas, exposure to storms will likely increase the number of

mass escapes. The frequency of extreme weather events such as storms in coastal and marine area is also increasing with global warming (IPCC, 2021). Without changing management practices the number of escapes is also likely to grow as a result of the greater number of salmon being produced.

Farmed Atlantic salmon are domesticated strains of Atlantic salmon with clearly identified genetic and developmental differences (Karlsson et al., 2016). They also significantly outnumber wild Atlantic salmon populations in major salmon producing countries, resulting in the number of escapes frequently being comparable to, or exceeding, the total wild population (Karlsson et al., 2016; Gilbey et al., 2021).



## Figure 2. 8 years of escapes data reported to the Norwegian government including the escapes for 2021 to date (Fiskeridirektoratet, 2021).

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Following escape, Atlantic salmon disperse into the marine environment rapidly, making any recapture unlikely (Uglem, Økland, and Rikardsen, 2012). The consequences of an escape are influenced by several factors, including the stage of development at escape, number of escapes, location, environmental conditions, the state of the wild salmon populations they interact with, and many more, making it challenging to predict how wild fish will be impacted (Bradbury et al., 2020; Heino et al., 2015; Castellani et al., 2018). But the interactions between escaped farmed salmon and wild conspecifics can broadly be divided into competition between escapees and wild salmon and genetic effects caused by hybridisation.

## Competition with wild fish

The impacts of escaped salmon are variable depending on the stage of development at which they escape. Evidence consistently shows that wild salmon have a higher fitness than escaped farmed salmon across their lifetime (Reed et al., 2015). However, escapes show varying levels of fitness relative to their wild counterparts at different stages of development. Experimental evidence suggests that in early freshwater stages of

development farmed salmon can sometimes outcompete wild salmon, possibly due to selective breeding for rapid growth (Sundt-Hansen et al., 2015). Glover et al., (2018) found that farmed salmon showed much higher growth than wild salmon in tanks, but only marginally higher growth in the wild when planted in a river as eggs and sampled over a four-year period, suggesting domestic salmon retain a level of phenotypic plasticity allowing them to adapt their morphology to circumstances. This shows that earlier escapes become better competitors with wild salmon than late escapes as they develop into a morphology closer to the wild phenotype, and this is theorised to be a response to food scarcity compared to the regular feeding on farms. Even when escapes show a lower fitness, their ability to compete at earlier stages of development reduces the food availability for wild counterparts leading to an overall population reduction (Skalaa et al., 2012).

Escaped salmon also change the population density in a river or near aquaculture facilities which can lead to increased predation pressure not just for salmon, but for all wild fish in the environment (Bradbury et al., 2020). One of the common reasons that escapes occur is because predators are attracted to the high fish density in aquaculture facilities

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and damage the nets trying to reach the fish (Callier et al., 2017). Escaped salmon frequently carry diseases at ahigher frequency than wild populations and may alter the incidence of diseases and parasites in wild populations following escape (Madhun et al., 2017: Bradbury et al., 2020). Several studies have demonstrated that farmed escapes do not persist at high concentrations in wild populations following a single escape (Wringe et al., 2018; Wacker et al., 2021). Selection pressures reduce the proportion of a population made up of farmed escapes year on year following large scale escape events, due to their lower competitive ability, but despite this the wild population still experiences a significant depression in following years because of the added competition. While ecological interactions outside of reproduction do present a serious challenge not just to wild salmon, but also to other wild fish, the greatest threat to the long-term survival of

Hybridisation and outbreeding

wild Atlantic salmon from farm

escapes is the production of hybrids.

#### depression

The domestication of Atlantic salmon has altered its genetic profile through four key mechanisms.

- The first is the founder effect. Farmed salmon strains have been bred from a small pool of founders leading to limited genetic variation within a strain. Most farmed salmon in Scotland and Norway are from lines based on source stock from a few Norwegian rivers (Karlsson et al., 2016; Glover at al., 2017).
- Second, farmed salmon are selectively bred for specific traits such as growth rate, disease resistance and age of maturation (Gjedrem, 2010). These characteristics are deliberately pursued to increase profits from aquaculture.
- The third mechanism is the adaptation of farmed salmon populations to the altered pressures of the aquaculture environment. Captive bred salmon for stocking, which have not been selectively bred but have been exposed to domestication pressures have been shown to have a lower fitness in the wild (McGinnity et al., 2009; Satake and Araki, 2011).
- Finally, genetic drift in isolation from wild Atlantic salmon allows for further genetic divergence (Glover et al., 2017). Domesticated salmon reared in the wild display a degree of phenotypic plasticity allowing them to develop into a morphology closer to a wild type

2016).

that under farmed conditions, but still display genetically determined physical differences from wild populations including those from which the original source stock for the domesticated strain was derived (Glover et al., 2018; Gutierrez, Yáñez, and Davidson,

Domestication has altered fitness related traits of Atlantic salmon in ways that dramatically reduce its survival and ability to reproduce in the wild (Bolstad et al., 2017). Sylvester et al., (2019) found that farmed escapes had a 0.15 chance of survival relative to their wild counterparts, while Skaala et al., (2019) estimated survival at 0.21 or 0.3 depending on the method of calculation. As the number of escapes each year frequently outnumbers the local population of wild Atlantic salmon, this still represents a large proportion of the total Atlantic salmon population in the wild.

**75%** NORWEGIAN SITES SHOWING GENETIC INTROGRESSION Escaped domestic salmon that survive long enough to spawn sometimes hybridise with wild salmon. Karlsson et al., (2016), in a study of approximately 75% of the total wild spawning sites in Norway, found genetic introgression of up to 42.2% in 51/109 sites.

**23.2%** 

#### **GENETIC INTROGRESSION**

Gilbey et al., (2021) in the first widescale assessment in Scotland found evidence of genetic introgression of Norwegian farmed salmon strains into wild Scottish salmon populations in 23.2% of surveyed sites, allowing that this is probably an underestimate. Many studies that have historically measured the number of escapes in a population and the level of introgression have relied on morphological cues such as body shape, but this is not an accurate method and likely to significantly underestimate the true numbers. suggesting older figures should be used with caution (Glover et al., 2018).

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Even genetic testing can produce underestimates. Gibley et al., (2021), used a methodology in which 54% of second-generation hybrids (the offspring of a domestic-wild hybrid and a wild fish) would be recorded as wild. The study used a modified version of the methodology in Diserud et al. (2020), but of the 237 sites analysed by Gibley et al., only 22 would have produced the minimum sample required by Diserud et al., (2020). This further shows that the level of introgression recorded, though already extensive, is likely an underestimate of the true extent. Even with limited sampling it is notable that this study was able to identify a continuous range of levels of genetic mixing showing multiple generations of hybridisation had occurred in some populations from chronic exposure to farmed escapes.

Glover et al., (2012; 2013) using a database of 22 Norwegian rivers, found that the ability of escaped farmed salmon to hybridize with wild conspecifics was highly dependent on the population density of the wild salmon, suggesting that only at a lower population density, and therefore lower level of competition to reproduce, were escapes able to participate in reproduction. There are examples of populations near

aquaculture farms that have yet to show any evidence of genetic introgression (Verspoor, Knox, and Marshall, 2016). However, Karlsson et al., (2016) and Gilbey et al., (2021), using much larger data sets found that the level of introgression was strongly correlated with the proximity to intensive salmon aquaculture and therefore the number of escapes entering a population. Heino et al., (2015) suggest there is an interaction between the volume of escapes and the demography of wild salmon populations, with diminishing populations more vulnerable to introgression. The timing of the escape is also important, as the earlier in development an escape occurs the more likely the escaped salmon are to participate in migration and then spawning (Skilibrei, 2010). Following an escape of 20,000 mature domestic salmon from Newfoundland, which is roughly equal to the wild population in the region, there was widespread hybridisation detected (about 27% and in 17/18 rivers), with a higher frequency of hybrids documented in smaller rivers (Wringe et al., 2018). As wild salmon populations continue to decline and aquaculture continues to expand, it is likely that the resistance of wild populations to further genetic introgression will reduce (Heino et al., 2015; Castellani et al., 2018).

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Compared to fish with pure farm genetics, hybrids have a higher fitness in the wild, but they still have a significantly lower fitness than wild salmon. Skaala et al., (2019) conducted an experimental study using over 250,000 eggs to compare the lifetime fitness of wild, hybrid and domestic salmon and found that first generation hybrids (F1) showed intermediate fitness between wild and domestic salmon. Wacker et al., in a study not limited to F1 hybrids, found between 49-70% lower survival in salmon with genetic introgression in a population with at least 20 years of genetic admixture. Wringe et al., (2018) and Sylvester et al., (2019)

found that the lower fitness of hybrids as a result of strong selection pressures against the maladaptive genes of domestic salmon led to a year-on-year reduction in the proportion of hybrids in a population without further escapes. However, there was still a reduction in the total wild population. Repeated exposure to escapes also leads to frequent genetic introgression, and therefore lower populations and further vulnerability to genetic introgression, which has led to concerns that this may trigger an extinction vortex in some populations (Verspoor et al., 2015; Castellani et al., 2018).

> Genetic introgression may trigger an extinction vortex in some populations

Image: from Getty Images

Sea lice are ectoparasites that go through mobile planktonic stages drifting in the ocean before attaching to a host and developing into mobile adult stages. Each species has a slightly different lifecycle, but all sea lice, once attached, feed on the mucus, skin and blood of salmon. The most commonly occurring species in European farmed salmon production is Lepeophtheirus salmonis, commonly known as the salmon louse, a specialist parasite of salmonids. The related generalist louse Caligus elongatus also infects Atlantic salmon in European production, while the specialist Caligus Rogercressyi, is the most significant sea louse species in Chilean production. The effects of sea lice are dependent on the infection pressure, the size and life stage of the salmon, and environmental conditions (Thorstad and Finstad. 2018). To account for this relationship, infection pressure from lice is often measured as the number of lice per gram of fish weight. A recent lab-based study that artificially infected wild salmon post smolts

found that after 28 days infected post smolts had a mean of 0.38 mobile lice g-1 (Fjelldal, Hansen and Karlsen, 2020). Infected post smolts had significantly lower growth rates across the 28 days and displayed osmoregulatory impairment indicated by increased plasma Na+ and Cl-, and infection was correlated with high cortisol levels and mortality. There were threshold values of lice intensity that lead to changes at 0.18 lice g-1 in Cl- and 0.22 lice g-1 in Na+, and generally moribund fish occurred at 0.2 lice g-1. This study does not replicate infection in wild fish or even farmed fish but does indicate likely trends in the physiological responses of salmon to sea lice infections.

**28 DAYS** TO SHOW SIGNIFICANTLY REDUCED GROWTH AFTER INFECTION WITH SEA LICE

Reduced growth resulting from sea lice infections is a well-established phenomenon in salmon farming, with one study estimating between 3.62-16.55% of potential biomass lost due to sea louse infections of salmon farms (Abolofia, Asche and Wilen, 2017). Susdrof et al., (2018) also found that the quantity of sea lice on wild salmon returning to spawn explained a significant amount of the variation in salmon condition and correlated with lower reserves of the lipids necessary to successfully migrate up stream. Many studies of wild salmon have shown that high levels of infection are associated with mortality in wild fish (Gargan et al., 2012; Berglund Andreassen, 2013; Taranger et al., 2014), but a recent study also demonstrated that the antiparasitic treatment itself used to test for salmon survival in the absence of sea lice has a negative fitness cost, suggesting studies have been consistently underestimating the rate of added mortality due to sea lice infection pressure (Bøhn et al., 2020).

It is also important to consider that the negative effects of sea lice on Atlantic salmon are often compounded by other environmental conditions. Exposure, even for a short period, to acidified water increases in the level of mortality when subsequently infected with sea lice (Finstad et al., 2007; 2012).

Salmon are also more vulnerable to sea lice-induced mortality in warmer years (Shephard and Gargan, 2020). Sea louse manipulation of the host salmon's immune system which aids in successful parasitisation, also increases susceptibility to Infectious Salmon Anaemia leading to much higher mortality during co-infection (Barker et al., 2019). Not only do salmon lice increase bacterial load and mortalities when a salmon is coinfected with *Piscirickettsia salmonis* but they also reduce the efficacy of the vaccine currently used to prevent outbreaks of this disease (Figueroa et al., 2017).

#### Transmission to Wild Atlantic Salmon

The extent of transmission of sea lice from farmed to wild Atlantic salmon populations and the effect that this has on wild salmon have both been debated for some time. Though sea lice naturally parasitise wild Atlantic salmon in low numbers it is well established that salmon farming conditions facilitate much higher density populations of sea lice that can then transmit between farms and into wild populations (Torrissen et al., 2013; Helland et al, 2015; Serra-Llinares et al., 2016). A study conducted from 2002-2007 found that the density of gravid sea lice in the water column correlated with sea

lice numbers on nearby farms, with a stronger effect around farms with higher biomass (Penston and Davies, 2009). Some studies have highlighted the difficulty in identifying the cause of death in marine salmon, as is it very hard to sample live marine juvenile salmon, and harder still to sample mortalities, making it challenging to establish a cause-andeffect relationship between sea lice from salmon farms and wild salmon mortalities (Kristoffersen et al., 2018). A study by Jackson et al., (2013) on Irish Atlantic salmon populations stands out for suggesting that sea liceinduced mortality is a limited (though still significant) factor in the marine mortality and conservation status of Atlantic salmon, because it increased the mortality of out-migrating smolts by around 1%. But Thorstad and Finstad (2018) dispute the statistical analysis of Jackson et al., (2013) and find their conclusions to be misleading, maintaining that because Atlantic salmon have such low rates of survival, that the difference of 1% in out-migrating populations is a loss of around 20% of the returning population, which will have a large impact on long term population dynamics. A later study in Ireland that analysed a 26-year record found that returns of one sea-winter wild salmon were 50% lower in years following high lice levels on nearby farms, highlighting that exposure to sea lice can also change survival-related behaviour (Shephard and Gargan, 2017).

It is possible to establish correlations and test the infestation pressure by experimentally dosing out-migrating juvenile salmon with anti-parasitic drugs commonly given to salmon as treatment for sea lice on farms. One study on approximately 75,000 smolts found that out migrating salmon treated with the antiparasitic sea lice treatment SLICE (containing emamectin benzoate) were 1.8 times more likely to return than untreated



salmon (Gargan et al., 2012). Another study on 30,000 smolts found that smolts treated using an antiparasitic bath treatment were 50 times more likely to survive in periods of outmigration with high lice infestation pressure, and that treated salmon were less likely to survive at very low lice infestation pressure because of a negative fitness cost associated with antiparasitic treatments (Bøhn et al., 2020). A study in Norway running from 1996-2008 found that treatment with antiparasitics had a significant positive effect on survival until spawning, with treated salmon 1.29 times more likely to survive than untreated salmon (Krkošek et al., 2013). This equates to an average of 39% fewer spawning adults owing to infection with sea lice. A metaanalysis that considered 188 separate releases of Atlantic salmon concluded that sea lice do contribute significantly to mortality during out migration, and that this interacts strongly with other environmental factors (Vollset et al., 2015).

**1888** Studies found a negative Effect on wild atlantic salmon mortality In a review of sea lice transmission in the larval stage Costello (2006) found studies dispersal of the planktonic stage ranging from 10km - 30km dependent on sea currents and predicts that true dispersal in higher currents may be up to 70km.

#### LARVAL SEA LICE CAN TRAVEL UP TO

**70 K M** A Scottish study found that wind

driven circulation was an important indicator of sea lice transmission between farmed and wild salmon as it created areas of different infectivity within the study loch (Amundrud and Murray, 2009). Another study found that transmission of sea lice and diseases between Scottish aquaculture was 75% greater going North compared to South because of prevailing conditions. (Adams, Aleynik and Black, 2016). Harte et al., found that the west coast of Scotland had predominantly L. salmonis while the east coast had mostly C. elongatus, and that the abundance of each was influenced by factors including temperature and salinity of the water (Harte et al., 2017). Higher sea temperatures lead to much more rapid growth and transmission in sea lice as their development is temperature dependent which makes local and seasonal temperature

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variation an important consideration, but also suggests that warming seas from climate change will alter the transmission dynamics of these parasites, and that the threat to wild fish is only growing (Vollset, 2019).Seasonal variation in louse pressure has also been shown to lead to reduced fitness in late outmigrating post smolts from some Norwegian fjords (Vollset et al., 2016). Of all the possible contributors to sea lice infection pressure of wild salmonids considered in a

comparative study however, infestation pressure from salmon farms was by far the most significant (Helland et al, 2015).

### Transmission to Sea Trout and Other Wild Fish

L. salmonis and C. elongatus also parasitise brown trout (Salmo trutta) in their anadromous form as sea trout. Gargan at al., (2016) estimated the background rate of infection away from aquaculture and found a consistent mean across three year of 3.6-3.8 mobile adult L. salmonis and 0.6-4.3 C. elongatus. However, unlike Atlantic salmon, sea trout remain in coastal waters close to their natal river which exposes them to the infection pressure of sea lice from aquaculture for much longer periods of time than migratory Atlantic salmon. Sea lice feed on the mucus, skin, and muscle of sea trout, as on Atlantic salmon, causing reduced growth, osmoregulatory stress, vulnerability to secondary infections and, at high rates of infection pressure, mortality (Thorstad et al., 2015). Wells et al., (2006) found threshold of 13 mobile lice per fish weighing 19-70g above which significant and abrupt physiological changes relating to stress occur. Several long-term studies have found the level of sea lice infection pressure on sea trout to be related to aquaculture production. Trout captured closer to fish farms were found to have higher levels of sea lice than those further away in several studies, up to 31km from farms, and those with higher lice counts had worse body condition (Moore et al., 2018; Shephard, MacIntyre and Gargan, 2016; Middlemas et al., 2012). Shephard, MacIntyre and Gargan, (2016) using a 25-year dataset with over 20,000 sea trout sampled across 94 lakes and rivers in Ireland, controlled for variable environmental conditions and background variation in population numbers, found that higher sea lice levels on sea trout were related both to proximity to aquaculture facilities and to higher temperature, which led to significantly reduced body condition. A study in Norway found that sea

trout experienced high levels of sea lice infections near salmon farms and that even in protected marine areas, established in regions with intensive aquaculture, sea trout had lice counts high enough to cause physiological damage, unlike sea trout sampled outside of areas with intensive aquaculture production (Bjørn et al., 2011).

The level of infection pressure also relates to the stage of production, with a higher weight of salmon on the fish farm, and the second year of twoyear salmon production cycles is associated with higher rates of sea lice on sea trout (Middlemas et al, 2010; Middlemas et al., 2012). Shephard and Gargan (2021) found, in a study of five rivers in Ireland, that when standardised sea lice counts are high on farms in April, there is a high probability of a below average subsequent sea trout run back into rivers, showing that the effects of sea lice pressure need to be considered in a local context, and that national treatment thresholds may not protect wild fish in many instances as counts of sea lice on farms are not always an accurate indicator of infection pressure on wild fish. Anadromy in brown trout is facultative and allows sea trout to gain weight on a rich ocean diet before returning to spawn with females having more and bigger

eggs as a result of their marine growth. However, infection with high levels of sea lice, which reduces growth and increases mortality, considerably reduces the advantage of entering the marine environment, leading to concerns that the pressuresof salmon aquaculture may lead to the establishment of exclusively freshwater populations of brown trout with lower overall genetic diversity (Thorstad et al., 2015).

Several studies have documented behavioural changes in sea trout in response to sea louse infection pressure. Because sea lice are marine parasites, they do not survive for very long at low salinities or in fresh water. This leads to the premature return of sea trout to their natal rivers or to lower salinity environments, which limits their ability to feed on rich marine food sources. Wells et al., (2007) tested the physiological effects of a return to freshwater on sea lice infected trout and found that it significantly reduced the degree of stress across all indicators measured, making it highly selected for behaviour. A study on artificially infected sea trout found that they returned to freshwater after an average of 18 days at sea, as opposed to an uninfected control group that spent an average of 100 days at sea,

and that infected fish also resided in the inner part of the fjord where the study was conducted, which is closer to fresh water (Sierra-Llinares et al., 2020). Gjelland et al., (2014) also noted a strong tendency in infected sea trout towards residing in shallow areas near the mouth of rivers and generally brackish or fresh water. They also found, confirmed by Halttunen et al., (2017) that a chemical sea louse treatment. emamectin benzoate (as an in feed treatment) in one study and a combination of emamectin benzoate injections and prophylaxes bath treatment in the other, increased survival in sea trout but did not stop behavioural changes in response to high infestation pressure. Given that treatment followed infection in both experiments, it was postulated that the behavioural adaptation of sea trout to infection is rapid and long lasting. Halttunen et al., (2017) modelled the implications of this behaviour and showed that it leads to

increased mortality, lower fecundity and reduced likelihood of sea migration in subsequent generations Several studies have documented behavioural changes in sea trout in response to sea louse infection pressure. Because sea lice are marine parasites, they do not survive for very long at low salinities or in fresh water. In Canada, the USA and Chile transmission of sea lice species (L. salmonis, C. rogercressyi, C. clemensi) to other Pacific salmonid species has also been documented (Zalcman et al., 2021). In Chile the abundance of C. rogercressyi shows biannual variation, with regular peaks in infection pressure on wild fish (Montes, Quiñones and Gallardo-Escárate, 2022). In Canada pink, chum, sockeye, Chinook and Coho salmon are all parasitised by sea lice that achieve high population densities on Atlantic salmon farms, though the degree of transmission has yet to be quantified for many populations (Beamish et al., 2005). Canadian

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studies have found that juvenile outmigrating sockeye salmon near salmon aquaculture facilities experience a combined level of infection an order of magnitude higher form L. salmonis and C. clemensi than those away from aquaculture, and that sockeye salmon experience significantly higher levels of osmotic stress than Atlantic salmon at the same infection pressure from L. salmonis (Price et al., 2011; Long, Garver and Jones, 2018). A three-year study in British Columbia found that parasite loads on pink and chum salmon are significantly lower during fallow periods of salmon farms but return to the same level as before fallowing after fallowing stops (Morton, Routledge and Williams, 2005). Morton, Routledge and Krkosek (2008) found that exposure to farms was the only significant predictor of sea louse abundance of pink and chum salmon after testing a range of environmental variables in a multi-year study. Beamish et al., (2005) observed differences between Pacific salmon species in the rate of chalimus and gravid stages of the two sea lice species L. salmonis and C. clemensi. Nekouei et al., (2018) found that salmon farms acted as an important source of sea lice for wild out-migrating chum salmon, but that infection levels on farms did not correlate with the infection level in

wild chum salmon, only the presence of sea lice, pointing to species specific host-parasite relationships and transmission dynamics. *C. clemensi* has also been found to infect Pacific herring, leading to complex networks of transmission between species, that are rapidly changing in response to warming oceans, making management of these parasites a complex task (Brookson et al., 2020; Godwin et al., 2020a).

Sea lice, though often framed primarily as a problem for wild Atlantic salmon, are having negative impacts on many other salmonid and non-salmonid wild fish populations. Notably, Atlantic salmon farms have a profound impact not just on the fitness of sea trout, but also on their behaviour, and the influence of high sea lice densities transmitted from farms is acting as a strong selection pressure against anadromy in brown trout. These phenomena are well documented in sea trout, but the impacts of the sea lice cultivated and dispersed by salmon farms on populations of other wild fish species are often still emerging. In combination with warming oceans and degradation of aquatic habitats, this represents a serious threat to the fitness of not just Atlantic salmon, but other fish species that interact with aquaculture.

#### **Sea Lice Treatments**

The average spring sea louse infestation cost Norwegian farms 9% of their profits in 2011 (Abolofia, Asche and Wilen, 2017). This would suggest that farmers have a strong incentive to reduce the sea louse population on their farms, but widely used treatment options are often expensive. Sea louse management practices cannot only be considered on the level of individual farms. Farms are connected in networks of transmission and management practices, where each farm can affect the abundance of sea lice in the whole network (Adams, Proud and Black, 2015). Synchronised treatments for sea lice are much better at reducing the total number of sea lice and preventing reinfection due to transmission between farms (Arriagada et al., 2017). Kragsteen et al., (2019) demonstrate that sea louse treatments can be considered a tragedy of the commons as transmission between farms makes not applying treatments at set thresholds damaging for the whole network of farms and the wild fish in their proximity, but beneficial to the individual farmer. Many of the major Atlantic salmon producing countries have regulations that require treatment once certain levels of

infestation on a farm have been reached which are explained in table 1. But these are often based around self-reporting systems with infrequent audits from regulators. Godwin et al., (2020b) analysed selfreported sea lice counts in Canada and found that in the months when counts were audited by external examiners from regulatory bodies the values were on average 1.95 lice per fish higher. Given that Canada's threshold for treatment is 3.0 lice (table 1) a difference of 1.95 will likely have a significant effect on the frequency with which costly treatments are applied. It is also worth noting that many of the drugs used to treat sea lice also have a withdrawal period, which means that salmon cannot be treated for a certain number of weeks leading up to harvest to ensure that the level of pesticides in the salmon sold to consumers is below a threshold set by food safety authorities, meaning sea lice are allowed to proliferate in the weeks immediately prior to harvest (McEwan et al., 2016; Hannisdal et al., 2020).

9%

PROFIT LOST ON NORWEGIAN FARMS TO SEA LICE IN 2011

SEA LICE	PAGE 20
NASCO	International goal is for "100% of farms to have effective sea lice management such that there is no increase in sea lice loads or lice-induced mortality of wild salmonids attributable to the farms".
Norway	Norway is divided into 13 production zones which operate on a traffic light-based system regarding sea lice numbers. Farmers are required to report their sea lice numbers weekly using a standardised counting method, along with sea temperature, sea lice treatments (include quantity of any drugs used), number of cleaner fish and results from sensitivity tests of lice to drugs, and then coordinate on control measures. The maximum limit before control measures must take place is 0.5 adult female lice (AF) and 0.1 AF in the spring during wild smolt migration into the sea. The Norwegian Food Safety Authorities (NFSA) can coordinate delousing operations, introduce stricter controls in certain areas, order slaughtering and fallowing, and reduce the maximum allowed biomass of sites that fail to properly comply. Sensitivity testing, managed by the Norwegian Veterinary Institute monitors sea lice sensitivity to pesticides.
Chile	The Servicio Nacional de Pesca y Agricultura (Sernapasca) introduced a national <i>C. rogercresseyi</i> national monitoring program in 2007. All active seawater farms (not just Atlantic salmon, Chile produces several finfish species that host <i>C. rogercresseyi</i> ) are required to randomly sample at least ten fish from each of four randomly selected cages every week and report lice counts. All developmental stages must be recorded. Sernapesca also collects weekly data on all disease events, mortality, lab testing, treatments and vaccinations as part of a national disease surveillance and control program.
Scotland	Weekly reporting is legally required as of March 2021. The government requires operators report to the Fish Health Inspectorate when they reach 2.0 AF, which leads to increased monitoring. If it exceeds 6.0 AF for less than 4 consecutive weeks and then drops below 2.0 AF nothing happens. If it is above 6.0 AF for less than 4 consecutive weeks but remains above 2.0 AF an advisory letter is issued and it counts as 1/2 breaches, if this continues for another 4 weeks, then it's 2/2 breaches and an enforcement notice is issued. If 6.0 AF is maintained for 6 consecutive weeks an enforcement notice is issued. A voluntary Code of Good Practice produced by Scottish Finfish Aquaculture advises thresholds for treatment should be 0.5 AF ( <i>L. salmonis</i> ) per fish from 1st Feb-30th June and 1.0 AF from 1st July-31st Jan.
Canada	In February all farms must perform sea lice counts in all pens and are required to enter the March-June period below 3.0 motile lice per fish (motile lice is all stages which are free moving e.g. pre-adult + adult, no male/ female differentiation). From March to June (the wild juvenile salmon outmigration period) if farmed fish have over 3.0 motile <i>L. salmonis</i> per fish they must report to the Department of Fisheries and Oceans (DFO) within 48 hours and take measures to reduce levels. From July to January monitoring continues and a sea lice management plan must be implemented above 3.0 motile lice, but there is not a threshold above which treatment is required to try and reduce stress. Most farms will still use treatments. Pre and post-treatment counts must be conducted and reported to DFO along with any suspected treatment failures. There are also routine counts year-round which must be reported monthly to DFO.

# Ireland The Marine Institute carries out regular inspection of sea lice levels on all fish farms according to the Monitoring Protocol (2000) and Strategy (2008) introduced by the Department of Agriculture, Food and the Marine. Every stock is inspected 14 times a year and results are published monthly to stakeholders and publicly released annually. Monitoring has been in place since 1991. The treatment threshold in the spring is 0.5 egg bearing females per fish and is synchronised with increasing temperature to disrupt the life cycle. Throughout the rest of the year the treatment threshold is 2.0 egg bearing females.

#### Faroe Islands

Executive order no.163 from 2009 requires counting every second week in summer and once a month in winter. There is no native population of Atlantic salmon, though salmon farming is one of the country's biggest exports. The limit was set at 1.5 egg producing lice/ salmon in 2017, down from 2.0 previously. In 2021 this will be reduced to 0.5 from 1st June- 31st July, and from 2022 onward to 0.5 from 1st May-31st July and 1.0 otherwise. A national vet can require treatments and coordinate these between different farms. All treatments must be recorded and reported.

Table 1. An overview of the sea louse reporting and treatment thresholds imposed in major salmon farming nations, and the standards set by the intergovernmental organisation the North Atlantic Salmon Conservation Organization (NASCO) for all nations to work towards, in order to limit the spread of sea lice between farms and into wild Atlantic salmon populations (NASCO, 2016; Zalcman et al., 2021).



Enforcing treatment thresholds and limiting sea lice numbers is becoming increasingly challenging as there is now evidence that L. salmonis has evolved at least partial resistance to every class of drug traditionally used to treat sea lice (Besnier et al., 2014; Helgesen et al., 2015; Myhre Jensen et al., 2020). Myhre Jesen et al., (2020) also showed that the frequency of resistance in the L. salmonis population correlates closely with the volume of each antiparasitic drug used on a two-year lag. These drugs will becoming increasingly less effective, the more they are used. Lice resistant to multiple treatment drugs have now been detected on wild Atlantic salmon and sea trout. suggesting that salmon farming is having a greater influence on the evolution of sea lice than wild salmonids (Fjørtoft et al., 2021). Following the discovery of resistance many indicators of sea lice resistance are being developed and in Norway regular tests of the sensitivity of lice to treatments are required (table 1).

New preventative methods for reducing sea lice pressure are being developed such as the use of plankton nets around the tops of cages which can reduce infection pressure by up to 30%, or snorkels cages, which keep salmon below the surface other than via a tube to access the surface allowing salmon to refill their swim

## bladders, and can reduce infection by

75%, but have raised concerns about limiting oxygen in the water (Grøntvedt, Kristoffersen and Jansen, 2018; Barrett et al., 2020a; Geitung et al., 2019). Another method now used for treating outbreaks is the use of hydro-licers or thermo-licers (washing fish with jets of fresh or hot water or using hyposaline treatments which salmon can withstand for longer than sea lice); however these have been associated with high fish mortality and sublethal stress (Overton et al., 2018; McDermott et al., 2021). In fact, Delfosse et al., (2020) found that handling salmon, a common element of treatment procedures subsequently increases vulnerability to sea louse infection. Studies have shown that resistance to sea lice is a heritable trait in Atlantic salmon and this might contribute to a future solution; however, it would take approximately ten generations of selective breeding to produce a resistant salmon, with the caveat that this may influence other traits that have been selected for by domestication (Gharbi et al., 2015). Many alternative methods are costly to introduce and may impact the development and survival of the farmed salmon. An approach that has gained much popularity especially in response to the declining effectiveness of chemical treatments, is the use of cleaner fish.

## **CLEANER FISH**

In response to the growing resistance of salmon lice to every chemical therapeutant traditionally used as treatments, many salmon farms now deploy large numbers of cleaner fish within the net pens to reduce lice numbers. Stocking cleaner fish is considered to be a good alternative to chemical treatments and other novel approaches because it is viewed as "salmon welfare-friendly" (Overton et al., 2019). However, acquisition and deployment of cleaner fish in salmon farms requires careful consideration as managing these species introduces several new problems.

Cleaner fish are a broad category of fish that remove ectoparasites or dead tissue through a mutualistic relationship with "clients". Some specialise such that the majority of their diet is acquired this way, however several species are also facultative cleaners that feed when the opportunity arises. Cleaner fish have been used in salmon farming since 1988 in Norway, but this was only on a small scale until other sea lice treatments began to fail (Treasurer, 2018). The species of cleaner fish used in Atlantic salmon aquaculture are described in table 2.

### Acquisition of Cleaner Fish

As salmon aquaculture grows, the demand for cleaner fish rises. Gentry et al., (2019) found across Norway, Scotland. Ireland and the Faroe Islands over 60 million cleaner fish are deployed a year. This figure does not consider stocking in Canada or Chile, two of the highest salmon producing countries globally, so it is safe to assume the true number is much higher. Due to concerns about cross contamination. cleaner fish are culled at the end of a salmon production cycle. Most of these cleaner fish are sourced from fisheries. An aquaculture industry is growing to meet the demand for cleaner fish, but currently only ballan wrasse and lumpsuckers are farmed, and these farms still predominately rely on wild fisheries for brood stock (Bolton-Warberg, 2017).

Though farmed cleaner fish are being proposed as a response to declining wrasse stocks, in a life-cycle analysis of the use of cleaner fish in salmon farms, Philis et al., (2021) found that using farmed ballan wrasse and farmed lumpfish had a significantly higher environmental cost than wrasse sourced from wild fisheries. This has led to concern about whether the harvest of cleaner fish for the use in aquaculture is sustainable.

Halvorsen et al., (2017) found that corkwing wrasse were significantly older and larger inside marine protected areas in Norway than out, after just a decade of large-scale harvesting. Setting size limits on catches to release younger fish is a common management strategy to relieve pressure on populations. However, an earlier study showed that sexual size dimorphism in wrasse species means that using size limits for selective harvesting will lead to sex specific harvesting (Halvorsen et al., 2016). This study found that all nesting goldsinny males in several populations sampled would have been harvested, once again suggesting overfishing may lead to rapid population crashes in these species. Not only is the rate of harvest making some populations vulnerable, but cleaner fish are often moved far from where they have been harvested. Faust et al., (2018) found that genetically distinct goldsinny wrasse were escaping sea cages where they had been deployed and hybridising with local populations.

Genetically distinct goldsinny wrasse escape the open net pen and hybridise with local populations

	Lumpsucker	Lives up to 14 years and displays strong sexual dimorphism with males reaching 40cm and females reaching 50cm. Reaches sexual maturity at around 3 years. Displays strong sexual dimorphism. Tolerant of colder temperatures than wrasse which is useful during winter salmon production phases. (Powell et al., 2018).
	Ballan wrasse	Lives up to 29 years, and are the fastest growing and largest wrasse growing up to 60cm. Larger size and robustness make them valuable for delousing later growth stages of salmon. There are two morphotypes with distinct life histories (may be subspecies, not confirmed). (Blanco Gonzalez and de Boer, 2017).
	Corkwing wrasse	Lives up to 9 years, reaches 28cm in length, and reaches maturity after 3 years. Strong sexual dimorphism with large nesting males compared to smaller females and sneaker males. (Blanco Gonzalez and de Boer, 2017).
•	Goldsinny wrasse	Lives up to 14 (males) to 20 (females) years and reaches maturity at 1-2 years, usually 10-12cm, up to a maximum of 18cm in length. Highly territorial with planktonic (as opposed to benthic like other cleaner fish) eggs. Genetic divergence detected in Norway. (Blanco Gonzalez and de Boer, 2017).
	Rock Cook wrasse	Lives up to 9 years and reaches 19cm in length. Males grow faster than females. Used earlier in the grow out cycles due to small size. (Blanco Gonzalez and de Boer, 2017).
	Cuckoo wrasse	Lives up to 17 years and reaches 35cm. Trialled early in experiments on the use of cleaner fish in salmon aquaculture, but not used frequently any longer. May make up part of the harvest in wrasse fisheries. (Skiftesvik et al., 2013).

Table 2. Overview of the biological characteristics of the primary species of cleaner fish deployed as a sea lice treatment in salmon aquaculture (Powell et al., 2018; Gonzalez and de Boer, 2017; Skiftesvik et al., 2013).

The welfare of cleaner fish during transport and after they have been deployed in salmon farms has also been called into question. A study on the welfare of rock cook and corkwing wrasse deployed in salmon farms found that their welfare measured by observing external harm did not decline significantly after stocking, but initial measurements after harvest demonstrated widespread damage, especially fin splitting in the caudal fin (Treasurer and Feledi, 2014). A later study on corkwing wrasse delousing in combination with other delousing methods also found consistently poor welfare (Gentry et al., 2019). An experimental study also found that ballan wrasse experience poor welfare under normal salmon aquaculture conditions as their physiology differs significantly from salmon and they are adapted to low flow, warmer environments (Yuen et al., 2019). In contrast lumpsuckers have been found to experience high levels of mortality in the summer as they are unsuited for the warmer climates where they are often deployed (Bolton-Warberg, 2017). Overton et al., highlight that cleaner fish frequently escape, are eaten by the salmon they share a sea cage with, are exposed to diseases, suffer stress and injury from handling during stocking and other sea lice treatments, and endure conditions to which they are poorly suited (2019). At the same

time, the evidence for how successful these species are at delousing suggests they may not be particularly effective.

Cleaner fish do eat sea lice, and some studies have shown stocking densities of 5-10% cleaner fish in salmon cages to be a helpful way of reducing sea lice numbers. But meta-analysis has shown that the effect of cleaner fish stocking on sea lice numbers has been very inconsistent, and many studies have only tested the effect of cleaner fish when they are deployed as part of a suite of methods, including chemical, used to try to combat rising sea lice numbers. Overton et al., (2019) found a range from 100%reduction of sea lice to a 28% increase in sea lice in studies examining the effects of stocking cleaner fish. A consistent finding is that the majority of cleaner fish do not actually feed on lice. Imsland et al., (2014) found that only 28% of lumpfish sampled had sea lice in their stomachs. Another study found only 11% of corkwing wrasse had sea lice in their stomachs (Gentry et al., 2019). Eliasen et al., (2018) found that lumpfish preferentially fed on alternative zooplankton sources when they were available in the summer months and fed on salmon feed as well as the lumpfish feed necessary to supplement their intended diet of lice. Lumpfish have been shown to be highly opportunistic feeders with a

preference for the most abundant food source, but many cleaner fish when sampled have no food in their stomachs as without training before deployment they do not act as cleaner fish even when no alternative food is available (Imsland et al., 2015; Eliasen et al., 2018).

A large-scale observational study on cleaner fish stocking in Norway found that stocking was associated with a short-term slowing of sea louse population growth that allowed salmon farms to wait an average of five weeks longer before using a different delousing treatment. However, this trend is a product of highly variable outcomes from stocking (Barrett et al., 2020b). The authors suggested that because stocking cleaner fish is often used in conjunction with other methods and in response to rising sea lice populations, it is difficult to ascertain the extent to which this trend is a result of stocking the cleaner fish, but that it seemed apparent that industry had not yet developed an effective method for deploying cleaner fish. Selective breeding for more efficient delousing in lumpfish has been proposed, but would take many generations to become useful (Whittaker, Consuegra and Garcia de Leaniz, 2021). In the meantime, both the individual cleaner fish and whole wild populations are being compromised.

Many of the cleaner fish harvested from the wild do not feed on lice at all

Salmon farms suffer not only from sea lice outbreaks, but also from a host of other parasites and pathogens (table 3) that proliferate in the aquaculture environment. The absence of natural predators in high density populations allows otherwise chronic diseases to become acute infections, changing endemic pathogens to epizootic outbreaks within farms (Krkošek, 2017). Many of the diseases that currently circulate in salmon farms have very similar symptoms leading to misdiagnosis and poor understandings of disease progression and transmission. For example, there are at least seven known causes of "marine salmon gill disease". These can produce symptoms individually or co-infect, generating "multifactorial gill disease" (Boerlage et al., 2020). Bouwmeester et al., (2021) identify five mechanisms through which salmon farming changes disease dynamics in wild fish populations:

1. Farmed species introducing diseases to an environment infecting wild conspecifics.  2. Farmed species introducing diseases to an environment infecting wild fish of other species.
3. Wild conspecifics infecting farmed fish which then amplify the load of the disease in the environment causing spill back to the hosts.
4. Wild conspecifics infecting farmed fish which then amplify the load of the disease in the environment infecting other wild fish species.
5. Farmed species changing the transmission dynamics without acting as a host.

The high mortality of many of these diseases makes it challenging to study transmission from farms to wild fish, as there is a strong likelihood that they would either be predated due to the lower fitness induced by disease or die before sampling. However, a growing body of evidence demonstrates that salmon farms are acting as reservoirs of disease that cause infections in wild salmon and other wild fish (Shea et al., 2020).

Disease	Cause	Symptoms	Source
Amoebic gill disease	The causative agent is the protozoan parasite <i>Neoparamoeba perurans</i> . It is widespread throughout many fish species.	Causes proliferative gill disease, leading to increased gill mucus, and patches of swollen tissue. Fish may swim close to the surface and breath rapidly.	Marine Scotland Directorate
Bacterial coldwater disease	Caused by the bacterium <i>Flavobacterium</i> <i>psychrophilum</i> . There is no effective treatment and growing antibiotic resistance, and new strains are emerging in aquaculture settings.	Juvenile fish have exophthalmia, haemorrhaging of abdominal areas, frayed fins and tail rot.	(Bruce et al., 2021; Staliper, 2011).
Bacterial Kidney Disease	The causative agent is the bacterium <i>Renibactterium</i> <i>salmoninarum</i> which can be transmitted horizontally by contact with infected fish, or vertically through eggs or sperm. There is no licensed treatment, so control on movement of fish is used. Identification of BKD is also challenging.	There may be no external symptoms, but symptoms include protruding eyes, darkening of skins, haemorrhage at the base of fins, pale anaemic gills and erratic behaviour. Internally there may be fluid accumulation in the abdominal cavity and kidney enlargement with cream/grey nodule on the kidney and possibly other organs.	(Jaramillo et al., 2017) and Marine Scotland Directorate
Cardio-myopathy Syndrome	The causative agent is piscine myocarditis virus thought to be related to the Totiviridae family. It was first identified in Norwegian aquaculture but has spread globally and into wild populations.	Fish often remain in good condition, and show little sign of infection before death, as symptoms are primarily internal. Diagnosis is based on lesions in the heart.	(Garseth et al., 2017a) and Marine Scotland Directorate

	It is still not well understood.		
Diplostomum spathaceum	The causative agent, <i>Diplostomum</i> <i>spathaceum, is</i> a parasitic fluke that lives in the eyes of freshwater fish towards the end of its life cycle.	Causes the development of cataracts, dark colouration and can lead to mortality.	(Klemme, Hyvärinen and Karvonen, 2021) and Marine Scotland Directorate
Enteric Redmouth/ Yersinosis	The causative agent is the bacterium Yersinosis ruckeri. This affects many salmonid species. There is an available vaccine.	Effects vary from unnoticeable to death. Infected fish show haemorrhaging at the tips of gills, ulceration and a red mouth caused venous and capillary congestion.	(Nguyen et al., 2018) and Marine Scotland Directorate
Epipheliocystis	This is a freshwater disease caused by primarily by chlamydia bacteria, but also several other pathogenic bacteria in at least 90 species of fish including Atlantic salmon. This is usually a benign infection.	Causes respiratory problems due to cysts on the gills and lesions, with high rates of mortality. Development is related to stress from unfavourable environmental conditions.	(Blandford et al., 2018) and Marine Scotland Directorate
Furunculosis	The causative agent is the bacterium Aeromonas salmonicida is airborne/ waterborne and can be introduced by healthy carrier fish. There is a vaccine, and antimicrobials can be used for treatment, and selective breeding has created resistance.	Causes septicaemia followed by boil like inflammatory lesions (furuncles) and death. Death can occur in cases with no outward signs. This was a major pathogen of aquaculture but is less challenging following effective management.	(Drangsholt et al., 2011) and Marine Scotland Directorate
Complex Gill Disease	There are at least seven known causes of gill disease (amoebic, parasitic, viral, bacterial,	Gill diseases are usually associated with impaired respiratory function from damage to the gills, and often mortality.	(Boerlage et al., 2020)

	zooplanktonic, harmful algal, and chemical/ toxin). When the cause is not obvious gill disease is referred to as complex gill disease. When there are many simultaneous causes it is multifactorial gill disease.		
Gyrodactylus Salaris	The small parasite <i>Gyrodactylus salaris</i> is present in much of Europe but not Scotland.	Infects parr, can cause a greyish appearance. Has been known to lead to 98% mortality in infected wild populations.	Marine Scotland Directorate
Heart and Skeletal Muscle Inflammation	The causative agent is Piscine orthoreovirus 1. Different strains of PRV-1 have different effects, only recent Norwegian strains of RPV-1 cause HSMI.	Typically occurs a few months following transfer to marine environment. Causes lesions on and inflammation of the heart, and necrosis of the red skeletal muscle.	(Wessel et al., 2020; Wessel et al., 2017)
Infectious Haemato-poietic Necrosis	The causative agent is a virus of the genus Novirhabdovirus, and transmitted through water, contact with contaminated untreated waste material, and equipment. Infected fish that survive act as carriers of the disease. It was first identified in American rainbow trout and now has been found infecting almost all salmonids around the world.	Causes lethargy with bouts of frenzy, dark colour, exophthalmia, pale gills, haemorrhaging at the base of fins, swollen abdomen.	Marine Scotland Directorate.
Infectious Pancreatic Necrosis	Caused by infectious pancreatic necrosis virus, an aquabirnavirus, it affects numerous species of fish and shellfish around the	Mortality occurs predominantly in juvenile stages, recently including post-smolts. All age groups and both freshwater and marine environments can sustain infection. It is	(Dopazo, 2020) and Marine Scotland Directorate

	world. It can be transmitted horizontally in fresh and saltwater, through waste and in dead bodies, and vertically. It is highly infectious.	often present asymptomatically. Causes abdominal swelling and internal pancreatic necrosis, and infected groups can suffer 80-90% mortality.	
Infectious Salmon Anaemia	The causative agent is the orthomyxovirus, infectious salmon anaemia virus. Only Atlantic salmon are susceptible, but rainbow trout and brown trout can be carriers. Transmitted through water, but primarily through live fish and discharge of untreated blood. No vaccine and no treatment are available.	There are two classes of ISAV: the nonvirulent ISAV-HPRO and the virulent ISAV-HPR∆. ISAV-HPRO is widespread in farmed salmon. ISVA- HPR∆ causes severe anaemia, haemorrhage in internal organs, ascites, darkening of the liver. The development of ISAV- HPRO into ISVA-HPR∆ is facilitated under aquaculture conditions.	(Rimstad and Markussen, 2020; Nylund et al., 2019) and Marine Scotland Directorate
Proliferative Kidney Disease	The causative agent is the myxozoan endoparasite Tetracapsuloides bryosalmonae. The parasite is widespread throughout salmonids in Europe and North America.	The development of PKD is temperature dependent, leading to concerns it will become more prevalent with climate change. Fish are dark, show exophthalmia, pale gills, distended abdomen, and poor development of the kidneys.	(Lauringson et al., 2021) and Marine Scotland Directorate
Red Vent Syndrome	The causative agent is suspected to be larvae of the parasitic nematode Anisakis simplex which is widespread in the digestive systems of wild salmon but causes disease at an abnormally high abundance in the event region.	RVS was first recorded in 2015 on returning salmon and has only been recorded in wild salmon to date but is suspected to have been caused by changes in parasite - host dynamics relating to warming ocean surface temperatures. RVS causes inflamed, bleeding vents and is most common in one sea winter returning salmon.	(Kent et al., 2020) and Marine Scotland Directorate

Salmoid Rickettsial Septicaemia/ Pisci- rickettsiosis	The bacterium <i>Piscicickettsia salmonis</i> is the causative agent of salmon rickettsial septicaemia, which is a major disease in Chilean aquaculture, and present but less severe elsewhere. It can survive for several weeks in seawater without a host. There are several vaccines, but their efficacy is questionable.	Causes lethargy, erratic behaviour, lack of appetite, darkening, skin lesions and ulcers. Clinical signs may be absent in infected fish. Cumulative mortality across grow out cycles has been recorded as high as 90%.	(Jones, 2019)
Salmonid alphavirus	7 genetic subtypes of the genus Alphavirus in the family Togaviridae are serious pathogens of farmed Atlantic salmon and other salmonids in Europe. SAV2 and 3 are the causative agent of Pancreas Disease (PD) in salmon in Norway, and SAV1, 4, 5, and 6 in the UK. It is transmitted through water.	In salmon SAV causes pancreas disease which results in lethargy, loss of appetite, abnormal swimming, high mortality, and in rainbow trout SAV2 causes rainbow trout sleeping disease. Mortality from PD can be up to 63%, and sublethal effects include significantly lower growth rates.	(Aslam et al., 2020) and Marine Scotland Directorate
Saprolegnia	Saprolegnia is a freshwater eukaryotic pathogen and an oomycete which are related to Chromista, chromophyte algae, and other Protista, not the fungi to which they are often compared. <i>Saprolegnia</i> <i>parasitica</i> is the most common causative agent.	Saprolegnia often occurs following vaccination of pre-smolt salmon against other diseases. It causes cotton wool like tufts growing from crescent shaped lesions and from the gills. This leads to lethargy, osmotic stress, and mortality.	(Beckmann et al., 2020) and Marine Scotland Directorate
Tenaci-baculosis/ yellow mouth/ mouth rot	Tenacibaculosis is caused by members of the flavobacteriaceae	Causes erosion and haemorrhaging of the mouth, development of	(Nowlan et al., 2021) and Marine Scotland

	family, notably	yellow plaques around the	Directorate
	Tenacibaculum maritimum, T. dicentrarchi and T. finnmerkense. It affects multiple marine species including Atlantic salmon and is, responsible for considerable aquaculture losses. There is no vaccine, it is treated with antibiotics.	mouth, ulcerative skin lesions, frayed fins, tail rot.	
Vibrosis	Vibrosis is caused by bacteria in the genus Vibrio, mostly commonly by <i>Listonella</i> <i>(Vibrio) anguillarum</i> in saltwater or brackish environments. Vibrio are a normal part of the gut microflora, but poor water quality and temperature changes trigger clinical outbreaks. Coldwater vibrosis (Hitra disease) is caused by <i>Allivibro</i> <i>salmonicida</i> , and many other Vibrios have been linked to fish diseases. An effective vaccine is widely used but does not prevent alloutbreaks. Following outbreaks antibacterial treatments are used.	Causes haemorrhagic septicaemia, muscle necrosis, anaemia, and skin lesions that rupture spreading blood and bacteria into the water. This eventually leads to mortality. Cold water vibrosis is less well understood, but also causes haemorrhagic septicaemia and high levels of mortality.	(Higuera et al., 2013; Nørstebø et al., 2018) and Marine Scotland Directorate
Viral Haemorrhagic Septicaemia	Viral haemorrhagic septicaemia virus is widespread through many wild fish populations and in farmed Atlantic salmon. Virus can be transmitted through water without direct contact.	Causes haemorrhaging in the eyes, kidneys, around the fin base and in muscles, connective tissues inflammation, a dark dorsal discolouration, and mortality.	(Lovy et al., 2013; Karreman et al., 2015) and Marine Scotland Directorate

Caused by <i>Moritella</i> <i>viscosa</i> among others. An effective vaccination against <i>M.</i> <i>viscosa</i> exists that protects against both development of symptoms and mortality.	Causes the development of ulcers on the skin, primarily the dorsal surface which grow gradually, and can lead to mortality.	(Karlsen et al., 2017)
	viscosa among others. An effective vaccination against <i>M.</i> viscosa exists that protects against both development of symptoms and	viscosaamong others.ulcers on the skin,An effectiveprimarily the dorsalvaccination against M.surface which growviscosaexists thatprotects against bothmortality.development ofsymptoms and

Table 3. Common diseases of Atlantic salmon that are found in aquaculture environments due to movement of pathogens between aquaculture facilities and wild fish.

# Salmon farms are acting as reservoirs of disease

Image: from Getty Images

## Transmission of Diseases to Wild Fish

Many diseases on salmon farms are transmitted through water, and so can travel long distances depending on the hydrogeography where a farm is situated. Because of the cost to aquaculture of these diseases, many of the studies on horizontal transmission of diseases consider infection dynamics between farms in close proximity. A study by Bang Jensen et al., (2020) found that Pancreas Disease (PD) caused by Salmonid Alphavirus (SAV) had a 30% chance of infecting other salmon farms 100km away if effective management is not introduced. This builds on an earlier study that found it takes an average of three months for a PD infection on a salmon farm to be detected and that the introduction of timely culling on farms to prevent spread would reduce the number of outbreaks by 57% a year (Aldrin, Huseby and Jansen, 2015). The transmission of diseases through water is not limited to PD. 50% of Infectious Salmon Anaemia (ISA) outbreaks were accounted for by transmission from neighbouring farms in another study (Aldrin et al., 2021). Jones et al., (2015) found that the risk of exposure to SAV and ISAV is directly related to the biomass of an infected farm and inversely related to the distance from a farm.

Movement of disease between farms can sometimes be accounted for through poor biosecurity practice and the movement by humans of equipment and fish between farms. However, studies have also confirmed the transmission of salmon diseases in a marine environment, which often do not require any direct contact and have shown movement into wild fish populations. In Tasmania, an experimental study on Pilchard Orthomyxovirus (POMV) found that POMV is highly transmissible from infected to naïve Atlantic salmon through seawater, without the need for any direct contact (Samsing et al., 2020). Salmon Gill Pox Virus (SGPV) is very common in Norwegian farmed salmon; a recent observational study suggests it is an important source of the virus in wild Atlantic salmon and sea trout (Garseth et al., 2017b). A Scottish study that screened for several known pathogens of farmed fish in wild Atlantic salmon found limited but significant evidence in the study population for the transfer of Infectious Pancreatic Necrosis virus (IPNV) from farmed to wild salmon and though transmission could not be confirmed found Viral Haemorrhagic Septicaemia virus (VHSV) and SAV in other both farmed salmon and nearby wild fish species (Wallace, McKay and Murray, 2017). Despite finding limited evidence of disease transfer in this study, they also noted that historically

there have been significant losses in wild Atlantic salmon populations from furunculosis and Bacterial Kidney Disease (BKD) attributed to transmission from salmon farms.

Interspecific transfer of diseases poses a serious threat to wild fish. Heart and **Skeletal Muscle Inflammation** (HSMI), which was first identified on Norwegian salmon farms, has now been detected spreading from farmed Atlantic salmon in British Columbia to Pacific salmon where it is has a demonstrable effect lowering fitness and survival in salmon with more challenging spawning migrations (Morton et al., 2017). This study found wild Pacific salmon near salmon farms were 32-40% more likely to have HSMI, and another study in British Columbia found that Chinook salmon near salmon farms were also significantly more likely to have Piscine Orthoreovirus (PRV) which also originated in Norwegian salmon farms (Mordecai et al., 2021).

Studies on eDNA, the DNA floating freely in the marine environment which is not associated with fish, have demonstrated that salmon farms can act as a reservoir shedding large quantities of viable pathogens into the marine environment around farms (Shea et al., 2020). This is an emerging technology to detect the abundance of pathogens and parasites but has already been shown to be a more accurate predictor of parasite and pathogen load in the water column than water quality indicators (Bastos Gomes et al., 2017; Peters et al., 2018). Studies using eDNA have suggested that salmon farms pose a serious risk to wild Atlantic salmon and other vulnerable wild fish because of their capacity to introduce high levels of pathogens into the environment (Shea et al., 2020; Bastos Gomes et al., 2017).



## Emerging Diseases in Aquaculture

Aquaculture environments have also been demonstrated to change pathogens from low virulence endemic strains to highly virulent strains with much higher rates of mortality. Kibegne et al., (2019) review into the emergence of novel viral diseases across the aquaculture sector found that "viral tourism"- the transfer of viruses through trade of biological material between salmon farms- has been responsible for the spread of several important diseases including VHSV, ISAV, SAV, and PRV, introducing these diseases to novel environments and hosts and facilitating the evolution of new strains. An example of this is HSMI, which was first diagnosed on salmon farms in 1999, and was later found to be caused by PRV-1. PRV-1 can be separated into two genetically distinct lineages, one of which has a low virulence, and the other of which causes HSMI (Dhamotharan et al., 2019). Another study found that ISAV, which also has low and high virulence strains, is widely present in both wild and farmed Atlantic salmon. However, salmon farm conditions select for the transition from low to high virulence strains, causing outbreaks of Infectious Salmon Anaemia (Nylund et al., 2019).

The importance of aquaculture conditions in facilitating this change in pathogens was experimentally tested in zebrafish using the pathogen Flavobacterium columnare, which also infects Atlantic salmon. This sevenyear study found aquaculture conditions facilitated a shift towards high virulence at both short and longtime scales, with lasting evolutionary effects on the pathogen (Sundberg et al., 2016). An earlier study on F. columnare in salmon found increasing occurrence over 23 years in juveniles and that more virulent strains could maintain infectivity for months after host death reducing the fitness cost of host death especially in high population density environments that facilitates easy transmission (Pulkkien et al., 2009). A lab study on Amoebic Gill Disease (AGD) in salmon also found that higher stocking densities selected for more virulent strains of AGD. In this case a higher stocking density led to mortalities from AGD at 23 days as opposed to 29 in the lower stocking density sample. Given that there are still frequently emerging cases of disease outbreaks with unidentified causes, this mechanism for developing highly virulent diseases is clearly a growing threat to wild fish (Currie et al., 2022).

## THE WIDER ENVIRONMENT

Varying conclusions in studies on the impacts of aquaculture on marine biota suggest that the responses of an ecosystem and its components to the presence of an aquaculture facility are often highly specific to the local context. Callier et al., (2017) highlight the fact that the effects of salmon farming on wildlife will change according to the size of the farm, the management choices, but also seasonally and with rising ocean temperatures, and that differences in interactions may be observed between day and night, at different depths or horizontal distance from the facility, and according to the local hydrogeography. Casadevall et al., (2021) note that the currently limited and sometimes contradictory scientific evidence makes it impossible to minimise ecological and environmental damage associated with aquaculture. If salmon farming expands into new habitats, as industry leaders have stated is their aim. the consequences are challenging to predict.

## Organic and Nutrient Enrichment of the Benthos

One of the consistent interactions that open net salmon farming has with the immediate environment is the depositing of large quantities of organic matter in the form of fish faeces below the cage. Ford et al., (2012) propose that the impact of this fallout should be assessed using multiple measures by considering -1. The area changed by farm organic waste

 2. The change to the nutrient concentration in the water column
3. The percentage of the carrying capacity of the local environment this reaches

4. The percentage of the total anthropogenic nutrient input made up by farm waste

to develop a clear picture of the scale of impacts from organic and nutrient enrichment by salmon farms.

Oh et al., (2015) found impacts of nutrient input on the benthic community extended on average 100-400m from farms. Mente et al., (2010) however, in a study on Scottish sea lochs found no effect after 2000m from farms. Several studies have pointed out that the distribution of organic material and nutrients is dependent on the hydrogeography of the site (depth, current speed, slope) and the degree of resuspension (Brigolin et al., 2009; Carvajalino-Fernández et al., 2020). The flow rate of the site also alters the distribution of the nutrients and organic waste, with high flow regimes distributing these further, leading to lower concentrations across a greater area (Keeley, Forrest and Macleod, 2013).

Where high concentrations of organic enrichment do occur under the salmon farms, large scale changes in the benthic community can be observed. As soon as salmon farming activity begins, changes are observed. These changes include a reduction in species diversity, particularly of crustaceans and bivalves, and an overall decrease in biomass of the communities, but an increase in the abundance of specialists that can withstand high organic input (Villnäs, Perus and Bonsdorff, 2011). This study also found that after farming stopped, though there was some recovery of species, the community structure and function had altered. Tucca et al., (2017) also found in a study on the bacterial community response to salmon farming that large shifts in the community structure persisted even after 35 months of fallowing. A study of the whole benthic community found that it took five years after salmon farming stopped at a site for benthic recovery to be almost complete (Keeley et al., 2014). The ability of a habitat to recover is highly dependent on whether there are appropriate colonisers nearby to repopulate as conditions become more favourable. However, salmon farming not only releases large quantities of organic waste, but also chemicals.

## Chemical Effects on the Benthos

Salmon are treated with large quantities of pesticides and antibiotics to try and prevent or treat sea lice and disease outbreaks that regularly cause mass mortalities on salmon farms. The nets are also treated with antifouling compounds to prevent build-up of algae. In turn these chemicals are dispersed freely into the surrounding environment where

they interact with wildlife. The main forms of antiparasitic drugs administered to salmon during the growth of salmon aquaculture have been organophosphates, pyrethroids, avermectins, and hydrogen peroxide. Most are applied through bath treatments where salmon swim in a certain concentration of these chemicals for a set amount of time. and then the treatment is washed into the sea. Emamectin benzoate, a commonly used avermectin, can be administered as an in-feed treatment which enters the environment though uneaten feed or in faeces (Urbina et al., 2019).

Because these chemicals are intended to target the ectoparasitic sea lice, which are crustaceans, other marine crustaceans are particularly vulnerable to the effects of these pesticides. Different chemicals have different toxicities. Azamethiphos, a commonly used organophosphate, affected amphipods 100m from a farm after 48 hours and at the same concentration azamethiphos causes

33% mortality in adult American lobsters and at a much lower concentration can still cause 80% mortality in the crab species Metacarcinus edwardsii (Ernst et al., 2014; Gebauer et al., 2017). Azamethiphos has been found to be considerably less harmful to marine crustaceans under normal use than the pyrethroid deltamethrin (Parsonset al., 2020; Burridge et al., 2014). Deltamethrin can cause mortality in American lobsters in the order of 10km away from where a treatment has been discharged, and has a half-life of 140 days allowing it to settle in benthic sediment (Page and Burridge, 2014; Ernst et al., 2014). The method of exposure can also change the effect with particulate deltamethrin settling in sediment having a much greater impact on functional groups that feed on particulate matter, as opposed to aqueous deltamethrin (Van Geest, Burridge and Kidd, 2014). Azamethiphos and deltamethrin have both been found to induce negative behavioural changes and death in a

Sea lice treatments are released into the environment at concentrations that kill wildlife

range of organisms at below the concentrations used in sea louse bath treatments (Urbina et al., 2019; Parsons et al., 2020; Bamber et al., 2021). Treatments are not always used independently, and treatments from neighbouring farms may mix in the marine environment. Frantzen et al., (2020) found that deltamethrin, azamethiphos and hydrogen peroxide had an additive effect, causing higher levels of mortality in combination.

### **Marine Mammal**

#### Deterrence

Marine mammalian predators, such as seals (pinnipeds) and dolphins (cetaceans) are often attracted to aquaculture facilities because of the concentration of fish within the nets. but also the abundance of sea life associated with changes to the benthic community, the higher population density of wild fish species that are attracted by the net structure and excess food in the environment around pens (Callier et al., 2017). Both mammals and bird species have been recorded damaging and becoming entangled in nets, which is costly for the salmon farmers. Therefore, various methods are used to deter marine predators. In February 2021 the Scottish government stopped granting licences to shoot seals for the prevention of serious damage to fish farms, or to protect the health and welfare of farmed fish, partly due to the decline in Harbour seal populations (Seal licensing – gov.scot, 2021). The main driver for introducing these new regulations, however, was to meet the requirements to sell salmon to the US market (Salmon Scotland, 2021). Nonlethal management techniques include the use of net tensioning, seal blinds, and acoustic deterrent devices (ADDs), also known as acoustic harassment devices (AHDs).

#### A BAN ON SHOOTING SEALS WAS INTRODUCED IN FEBRUARY

2021

Seal blinds are a thicker material covering an area at the base of the net to obscure dead fish that accumulate and attract seals to the bottom of the net. These have proved challenging to maintain for farmers as the seal blind can limit the rate of waste materials passing through the net and catch the current causing the net to become distorted (Northridge, Coram and Gordon, 2013 - p.34).

ADDs emit intense sounds within the hearing range of their target species, usually pinnipeds, to deter them from using a space. A range of different options exist that are positioned on cages under water, often with multiple devices in a single farm that may be set to run continuously (Findlay et al., 2018). The Aquaculture Stewardship Council (ASC) Salmon Standard prohibits certified salmon farms from using ADDs because of the associated negative effects on marine wildlife (ASC, 2019 - pp.20-22). ADD noise has been linked to reductions of the hearing sensitivity of non-target marine mammals such as harbour porpoises, sometimes permanently, and can cause them to stay away from areas used for foraging, breeding, or resting with

unknown long-term consequences for individuals and populations (Findlay et al., 2018). There have been studies conducted trying to reduce the impact of ADDs on non-target species by using frequencies that cetaceans are less sensitive to, but with very limited datasets it is challenging to draw conclusions (Götz and Janik, 2014). There has been some progress towards regulating the use of ADDs in Scotland requiring the use of "new generation" devices that will only theoretically affect pinnipeds and must meet the regulatory threshold of not "an injury that is more likely than not to lead to the death of the affected marine mammal" (SSPO ADD Statement, 2021; Ace Aquatec, 2021).



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The impacts of salmon farming on the immediate environment and the organisms passing through are an important element of a larger picture. As with any large scale, global industrial activity, many of the environmental impacts of salmon farming are not immediately evident because they are a result of processing and feed production. A frequently used method for considering the sustainability of a product is a life cycle analysis (LCA), which consider a range of environmental impacts across the entire production cycle. Many LCA studies conducted to determine the environmental effects of farmed salmon have highlighted that most of the greenhouse gas emissions, ozone depletion potential, eutrophication potential and other negative environmental impacts of salmon farming are a result of acquiring and processing the material to make feed for salmon (Sherry and Koester, 2020; Ellingsen, Olaussen

and Utne, 2009). LCA studies of food sources were developed as a way of accounting for the globalisation of production but have historically been geared towards terrestrial production and often struggle to account for biodiversity impacts as they are not interchangeable in the way that CO2 emitted anywhere will have a roughly similar effect. Therefore, LCAs of salmon farming frequently do not address, let alone attempt to quantify, the impacts of salmon farming on the ecosystems it inhabits. A recent metaanalysis conducted on LCAs of salmon farming found the methodologies were so inconsistent that comparison and drawing useful conclusions was challenging (Philis et al., 2019). Despite these inconsistencies, each methodology has demonstrated a similar trend in identifying feed production as the highest contributor to the environmental footprint of salmon production.

#### **Feed Production**

As the salmon farming industry has grown, with production increasing from 230 thousand tonnes in 1990 to 2.7 million tonnes of live weight salmon in 2020, the percentage of marine ingredients included as fish meal and fish oil in salmon feed has fallen (Iversen et al., 2020; GLOBEFISH, 2021). It has reduced from approximately 90% in 1990, to <30% now in conventional salmon farming, though organic salmon farming requires a higher input of marine fish meal and fish oil (Ytrestøyl, Aas and Åsgård, 2015). Using large quantities of fish meal and fish oil, derived from ocean fisheries is considered by some to be hugely inefficient because the volume of fish consumed by salmon in much greater than the volume of salmon produced at the end of the harvest, as is true of every higher trophic level species (Naylor et al., 2009). As there is a limited global supply of fishmeal and oil, most species harvested for these products are fully or over exploited, and some species traditionally used to produce fish meal and oil are now being consumed more by humans (Olsen and Hasan, 2012). This competition for resources created concern that not only is the production of fish meal and fish oil contributing to unsustainable overfishing, but also taking a food

source from people who traditionally fish the species now being used as food for Atlantic salmon such as pelagic fish in Senegal and The Gambia, India and Peru (Changing Markets Foundation et al., 2021). However, any supplement used for fishmeal or fish oil must still have a similar nutrient profile to adequately meet the needs of growing salmon.

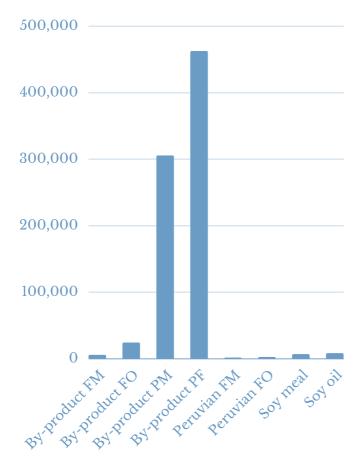
Torrissen et al., (2011) argue that fish meal and fish oil are now frequently made with by-products from fisheries for human consumption and that the increasing plant material supplementing salmon feed makes salmon one of the "most sustainable meat products", while at the same time arguing that plant protein in salmon feed is less sustainable than others have claimed. However, the argument that feed ingredients derived from by-products and plants are more sustainable needs further consideration. A recent comparative LCA considering different aquafeed ingredients found that ingredients performed differently across different categories, as expected, but that by-products from fish for human consumption converted into fishmeal and fish oil had a higher global warming potential than fish meal and fish oil from purpose harvested fisheries (Silva et al., 2017). In fact, all the alternative ingredients proposed

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(by-product fish meal and fish oil, byproduct poultry meal and fat, and soy meal and oil) performed worse than conventional fishmeal and fish oil across every metric, with soy meal and oil sometimes giving comparable but marginally higher values. Whilst the method of accounting can have a large impact on the results of a LCA, this demonstrates that by-product substitutions are not the silver bullet they are often presented as.

Figure 3. The global warming potential (GWP) in kg CO2 eq per 1t of ingredients commonly used in salmon feed including fish meal (FM), fish oil (FP), poultry meal (PM) and poultry fat (PF). Data based on life cycle analysis by Silva et al., (2017).



#### BETWEEN 2006 - 2015 THE OMEGA-3 CONTENT OF FARMED SALMON HAS FALLEN BY

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One proposed solution is to increase the proportion of plant material in feed. This has proved challenging for the aquaculture industry as plant feeds do not typically contain the same nutrient profile as marine sources of feed leading to a changing nutrient profile in harvested salmon. The content of omega-3 fatty acids, which are promoted as an important health benefit of consuming salmon, halved between 2006-2015 in Scottish salmon (Sprague, Dick and Tocher, 2016). The development of transgenic crops to produce terrestrial omega-3s for salmon feed has made progress, but still requires combination with fish oil (Betancor et al., 2015). Cadillo-Benalcazar et al., (2020) consider the possibility of plants and insects as a source of feed and find that both have considerable vulnerabilities because of the processing and land required to make suitable feed. It requires

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significant processing to produce a feed from plants with a high enough fat and protein content, and low enough fibre and anti-nutrient content to enable salmon to grow and develop normally. Most of the plantbased feed ingredients currently used in Scottish salmon production come from South America and are transported huge distances (Newton and Little, 2017). Whether this could be considered truly sustainable, rather than marginally better than feed produced from primarily marine ingredients is not yet clear.

Another alternative to fish meal and fish oil derived from pelagic fish that has been proposed during the expansion of salmon farming is meal and oil produced from krill (a group of 85 species) and particularly Antarctic krill, Euphausia superba (Olsen et al., 2006; Mørkøre et al., 2020; Kawaguchi and Nicol, 2020). Antarctic krill is a keystone species, meaning it is disproportionally important to the functioning of the Antarctic ecosystem relative to its biomass (Kawaguchi and Nichol, 2020). Krill meal and oil have nutrient profiles closer to fish meal and oil than plant-based sources, although Olsen et al., (2006) found that salmon have a lower feed conversion ratio when fed krill-based feed than when given fish based feed.

greater mass of krill must be consumed by salmon for them to grow at the same rate as fish-based feed. Krill fisheries are growing in response to demand and because climate change is reducing winter sea ice, allowing krill fisheries to operate year-round, where previously activity was limited in winter (Kawaguchi and Nichol, 2020). Krill meal and oil have similar environmental costs to fish meal and oil (Draganovic et al., 2013; Song et al., 2019). The distances travelled to harvest krill are great enough to make krill meal and oil more expensive than fish meal and fish oil, and it is being considered as an alternative ingredient for aquaculture only because pelagic fish are already being harvested at, and sometimes beyond, a sustainable limit (Mørkøre et al., 2020; Draganovic et al., 2013). The combined impacts of climate change and increasing harvest are causing concerns for not only krill populations, but also the ecosystems dependent on them (Schiermeier, 2010). Krill meal and oil may be marginally more sustainable than fish meal and oil according to some metrics, but they also have considerable environmental and ecological costs that will scale with use as a feed ingredient.

Due to the higher chitin content a

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Various metrics are used to assess the sustainability of salmon relative to other food sources based on feed consumption, such as the fish in: fish out ratio (FI:FO), the Feed Conversion Ratio (FCR), and the Marine Nutrient Dependency Ratio (MNDR) which indicate how salmon convert marine input into salmon ready for sale (Ytrestøyl, Aas and Åsgård, 2015). Advances in processing soy, wheat and rapeseed to make digestible plant-based protein and fat sources for salmon feed have considerably reduced each of these ratios, however, advances in feed production that make it more sustainable must be weighed against the massive expansion of the industry, because this still results in an absolute increase in resource use. This includes marine resource use, the acquisition and processing of which is

widely accepted to have the greatest negative environmental impact of any part of salmon farming in LCAs (Naylor et al., 2009). Troell et al., (2014) also highlight that using terrestrial sources of fat and protein typically reduces the resources available for terrestrial animal agriculture, so considering salmon as a source of marine protein additional to the production of terrestrial protein can be highly misleading. Atlantic salmon, as a carnivorous fish requires a large input of fat and protein to grow and develop into a product that salmon farmers can sell. Whatever the source of the ingredients, that absolute amount of nutrients required to produce salmon will not fall, and salmon will continue to be a resource intensive, net consumer of food.



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#### CONCLUSIONS

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## CONCLUSIONS

Open net salmon farming has introduced acute and chronic threats to wild Atlantic salmon populations and other species of wild fish.

- Escapes cause acute threats from competition during large scale escapes. The escaped salmon outnumber wild populations.
- Escapes cause chronic threats from outbreeding depression and hybridisation. Wild salmon are already experiencing enough of a decline that populations do not have the resilience to wait the 50 years it would take to recover genetic fitness, especially when exposed regularly.
- Sea lice are a chronic threat to wild Atlantic salmon, other salmonids, and *C. elongatus* are a threat to many other wild fish too, reducing the fitness of individuals and causing greater vulnerability to other threats.
- Cleaner fish are subject to chronic threats from over-harvesting of populations, and general welfare concerns without proven benefit.
- Diseases are a chronic threat to wild salmon and other wild fish because of exposure to greater

infection pressure from a greater number of diseases.

- Diseases cause acute threats through the introduction of novel diseases because of transmission globally through aquaculture networks and from the development of more virulent strains of endemic pathogens.
- The wider environment suffers acute threat from deposition of nutrients and organic matter changing benthic community structures and the spread of antiparasitic drugs killing (commercially important) crustaceans.
- The wider environment suffers chronic threat from community structure remaining changed and community function being impaired because of missing species, and exclusion of megafauna such as whales.
- There are chronic threats to sustainability from a growing aquaculture industry that relies on harvesting wild fish for feed and for which currently the only alternatives are land and water intensive crops that need massive processing to create useful feed.

The salmon industry has tried developing novel technologies and methods to reduce the many known harms. But a system that is reliant on the large-scale harvest of marine resources to support the production of a carnivorous fish, under conditions known to facilitate parasite and disease outbreaks, with harms that are then easily spread to the wider environment, will always have a cost for wild fish and their wider environment.

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- Abolofia, J., Asche, F. and Wilen, J.E. (2017). The Cost of Lice: Quantifying the Impacts of Parasitic Sea Lice on Farmed Salmon. Marine Resource Economics, 32(3), pp.329–349.
- Ace Aquatec. 2021. Predator Control Award Winning Deterents | Ace Aquatec. [online] Available at: <a href="https://aceaquatec.com/products/predator-control/">https://aceaquatec.com/products/predator-control/</a> [Accessed 12 October 2021].
- Adams, T., Aleynik, D. and Black, K. (2016). Temporal variability in sea lice population connectivity and implications for regional management protocols. Aquaculture Environment Interactions, 8, pp.585–596.
- Adams, T., Proud, R. and Black, K. (2015). Connected networks of sea lice populations: dynamics and implications for control. Aquaculture Environment Interactions, 6(3), pp.273–284.
- Addressing impacts of salmon farming on wild Atlantic salmon: Challenges to, and developments supporting, achievement of NASCO's international goals. 2016. Report of a Theme-based Special Session of the Council of NASCO. NASCO Council document CNL(16)60. 196pp
- Aldrin, M., Huseby, R.B. and Jansen, P.A. (2015). Space-time modelling of the spread of pancreas disease (PD) within and between Norwegian marine salmonid farms. Preventive Veterinary Medicine, 121(1-2), pp.132–141.
- Aldrin, M., Huseby, R.B., Bang Jensen, B. and Jansen, M.D. (2021). Evaluating effects of different control strategies for Infectious Salmon Anaemia (ISA) in marine salmonid farming by scenario simulation using a disease transmission model. Preventive Veterinary Medicine, 191, p.105360.
- Amundrud, T.L. and Murray, A.G. (2009). Modelling sea lice dispersion under varying environmental forcing in a Scottish sea loch. Journal of Fish Diseases, 32(1), pp.27–44.
- Aquaculture Stewardship Council Salmon Standard Version 1.2, 2019 pp.20-22 Arriagada, G., Stryhn, H., Sanchez, J., Vanderstichel, R., Campistó, J.L., Rees, E.E., Ibarra, R. and St-Hilaire, S. (2017). Evaluating the effect of synchronized sea lice treatments in Chile. Preventive Veterinary Medicine, 136, pp.1–10.
- Aslam, M.L., Robledo, D., Krasnov, A., Moghadam, H.K., Hillestad, B., Houston, R.D., Baranski, M., Boison, S. and Robinson, N.A. (2020). Quantitative trait loci and genes associated with salmonid alphavirus load in Atlantic salmon: implications for pancreas disease resistance and tolerance. Scientific Reports, 10(1).
- Bamber, S., Rundberget, J.T., Kringstad, A. and Bechmann, R.K. (2021). Effects of simulated environmental discharges of the salmon lice pesticides deltamethrin and azamethiphos on the swimming behaviour and survival of adult Northern shrimp (Pandalus borealis). Aquatic Toxicology, 240, p.105966.

Bang Jensen, B., Dean, K.R., Huseby, R.B., Aldrin, M. and Qviller, L. (2021). Realtime case study simulations of transmission of Pancreas Disease (PD) in Norwegian salmonid farming for disease control purposes. Epidemics, 37, p.100502.

Barker, S.E., Bricknell, I.R., Covello, J., Purcell, S., Fast, M.D., Wolters, W. and Bouchard, D.A. (2019). Sea lice, Lepeophtheirus salmonis (Krøyer 1837), infected Atlantic salmon (Salmo salar L.) are more susceptible to infectious salmon anemia virus. PLOS ONE, 14(1), p.e0209178.

Barrett, L.T., Oppedal, F., Robinson, N. and Dempster, T. (2020a). Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. Reviews in Aquaculture, 12(4), pp.2527–2543.

Barrett, L.T., Overton, K., Stien, L.H., Oppedal, F. and Dempster, T. (2020b). Effect of cleaner fish on sea lice in Norwegian salmon aquaculture: a national scale data analysis. International Journal for Parasitology, 50(10-11), pp.787–796.

Bastos Gomes, G., Hutson, K.S., Domingos, J.A., Chung, C., Hayward, S., Miller, T.L. and Jerry, D.R. (2017). Use of environmental DNA (eDNA) and water quality data to predict protozoan parasites outbreaks in fish farms. Aquaculture, 479, pp.467–473. Beamish, R.J., Neville, C.M., Sweeting, R.M. and Ambers, N. (2005). Sea lice on adult Pacific salmon in the coastal waters of Central British Columbia, Canada. Fisheries Research, [online] 76(2), pp.198–208. Available at:

https://www.sciencedirect.com/science/article/abs/pii/S0165783605001785? via%3Dihub.

Beckmann, M.J., Saraiva, M., McLaggan, D., Pottinger, T.G. and van West, P. (2020). Saprolegnia infection after vaccination in Atlantic salmon is associated with differential expression of stress and immune genes in the host. Fish & Shellfish Immunology, 106, pp.1095–1105.

Berglund Andreassen K. (2013) . Effects of infections with salmon lice (Lepeophtheirus salmonis) on wild smolts of salmon (Salmo salar L.) and trout (Salmo trutta L.) (in Norwegian), Norway University of Tromsøpg. 61 pp Master thesis

Besnier, F., Kent, M., Skern-Mauritzen, R., Lien, S., Malde, K., Edvardsen, R.B., Taylor, S., Ljungfeldt, L.E., Nilsen, F. and Glover, K.A. (2014). Human-induced evolution caught in action: SNP-array reveals rapid amphi-atlantic spread of pesticide resistance in the salmon ecotoparasite Lepeophtheirus salmonis. BMC Genomics, 15(1).

Betancor, M.B., Sprague, M., Sayanova, O., Usher, S., Campbell, P.J., Napier, J.A., Caballero, M.J. and Tocher, D.R. (2015). Evaluation of a high-EPA oil from transgenic Camelina sativa in feeds for Atlantic salmon (Salmo salar L.): Effects on tissue fatty acid composition, histology and gene expression. Aquaculture, 444, pp.1–12.

Bjørn, P., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R. and Kristoffersen, R. (2011). Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions, 1(3), pp.233–244.

Bjørn, P., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R. and Kristoffersen, R. (2011). Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions, 1(3), pp.233–244.

Blanco Gonzalez, E. and de Boer, F. (2017). The development of the Norwegian wrasse fishery and the use of wrasses as cleaner fish in the salmon aquaculture industry. Fisheries Science, 83(5), pp.661–670.

Blandford, M.I., Taylor-Brown, A., Schlacher, T.A., Nowak, B. and Polkinghorne, A. (2018). Epitheliocystis in fish: An emerging aquaculture disease with a global impact. Transboundary and emerging diseases, [online] 65(6), pp.1436–1446. Available at: https://www.ncbi.nlm.nih.gov/pubmed/29790651 [Accessed 24 Nov. 2019].

Boerlage, A.S., Ashby, A., Herrero, A., Reeves, A., Gunn, G.J. and Rodger, H.D. (2020). Epidemiology of marine gill diseases in Atlantic salmon (Salmo salar) aquaculture: a review. Reviews in Aquaculture, 12(4), pp.2140–2159.

Bøhn, T., Gjelland, K.Ø., Serra-Llinares, R.M., Finstad, B., Primicerio, R., Nilsen, R., Karlsen, Ø., Sandvik, A.D., Skilbrei, O.T., Elvik, K.M.S., Skaala, Ø. and Bjørn, P.A. (2020). Timing is everything: Survival of Atlantic salmon Salmo salar postsmolts during events of high salmon lice densities. Journal of Applied Ecology, *57*(6), pp.1149–1160.

Bolstad, G.H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O.H., Fiske, P., Jensen, A.J., Urdal, K., Næsje, T.F., Barlaup, B.T., Florø-Larsen, B., Lo, H., Niemelä, E. and Karlsson, S. (2017). Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nature Ecology & Evolution, 1(5).

Bolton-Warberg, M. (2017). An overview of cleaner fish use in Ireland. Journal of Fish Diseases, 41(6), pp.935–939.

Bouwmeester, M.M., Goedknegt, M.A., Poulin, R., Thieltges, D.W. and Pettorelli, N. (2021). Collateral diseases: Aquaculture impacts on wildlife infections. Journal of Applied Ecology, [online] 58(3), pp.453–464. Available at:

http://web.a.ebscohost.com/ehost/detail/detail?vid=3&sid=3a639db6-e5af-43fc-bc00-8f212165c6d1%40sdc-v-

sessmgr03&bdata=JnNpdGU9ZWhvc3QtbGl2ZQ%3d%3d#db=8gh&AN=149017029 [Accessed 28 Apr. 2021].

Bradbury, I., Burgetz, I., Coulson, M., Verspoor, E., Gilbey, J., Lehnert, S., Kess, T., Cross, T., Vasemägi, A., Solberg, M., Fleming, I. and McGinnity, P. (2020). Beyond hybridization: the genetic impacts of nonreproductive ecological interactions of salmon aquaculture on wild populations. Aquaculture Environment Interactions, 12, pp.429–445.

Brigolin, D., Pastres, R., Nickell, T., Cromey, C., Aguilera, D. and Regnier, P. (2009). Modelling the impact of aquaculture on early diagenetic processes in sea loch sediments. Marine Ecology Progress Series, 388, pp.63–80.

Brookson, C.B., Krkošek, M., Hunt, B.P.V., Johnson, B.T., Rogers, L.A. and Godwin, Sean.C. (2020). Differential infestation of juvenile Pacific salmon by parasitic sea lice in British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 77(12), pp.1960–1968.

Bruce, T.J., Ma, J., Jones, E.M., Vuglar, B.M., Oliver, L.P., Knupp, C., Loch, T.P. and Cain, K.D. (2021). Assessment of Flavobacterium psychrophilum -associated mortality in Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis). Journal of Fish Diseases, 44(5), pp.645–653.

Burridge, L.E., Lyons, M.C., Wong, D.K.H., MacKeigan, K. and VanGeest, J.L. (2014). The acute lethality of three anti-sea lice formulations: AlphaMax®, Salmosan®, and Interox®ParamoveTM50 to lobster and shrimp. Aquaculture, 420-421, pp.180–186. Cadillo-Benalcazar, J.J., Giampietro, M., Bukkens, S.G.F. and Strand, R. (2020). Multi-scale integrated evaluation of the sustainability of large-scale use of alternative feeds in salmon aquaculture. Journal of Cleaner Production, 248, p.119210.

Callier, M.D., Byron, C.J., Bengtson, D.A., Cranford, P.J., Cross, S.F., Focken, U., Jansen, H.M., Kamermans, P., Kiessling, A., Landry, T., O'Beirn, F., Petersson, E., Rheault, R.B., Strand, Ø., Sundell, K., Svåsand, T., Wikfors, G.H. and McKindsey, C.W. (2017). Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. Reviews in Aquaculture, 10(4), pp.924–949. Carvajalino-Fernández, M.A., Sævik, P.N., Johnsen, I.A., Albretsen, J. and Keeley, N.B. (2020). Simulating particle organic matter dispersal beneath Atlantic salmon fish farms using different resuspension approaches. Marine Pollution Bulletin, 161, p.111685.

Casadevall, M., Rodríguez-Prieto, C., Torres, J., Eira, C., Marengo, M., Lejeune, P., Merciai, R. and Richir, J. (2021). Editorial: Marine Aquaculture Impacts on Marine Biota. Frontiers in Marine Science, 8.

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T. and Glover, K.A. (2018). Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. Evolutionary Applications, 11(6), pp.1010–1025. Changing Markets Foundation, Feedback, Deutsche Umwelthilfe, L214, Aquatic Life Institute Europe, Acción Planetaria, Transición Verde and Carro de Combate (2021). Floundering Around: An assessment of where European retailers stand on the sourcing of farmed fish.

Costello, M.J. (2006). Ecology of sea lice parasitic on farmed and wild fish. Trends in Parasitology, 22(10), pp.475–483.

Currie, A.R., Cockerill, D., Diez-Padrisa, M., Haining, H., Henriquez, F.L. and Quinn, B. (2022). Anemia in salmon aquaculture: Scotland as a case study. Aquaculture, 546, p.737313.

Delfosse, C., Pageat, P., Lafont-Lecuelle, C., Asproni, P., Chabaud, C., Cozzi, A. and Bienboire-Frosini, C. (2020). Effect of handling and crowding on the susceptibility of Atlantic salmon (Salmo salar L.) to Lepeophtheirus salmonis (Krøyer) copepodids. Journal of Fish Diseases, 44(3), pp.327–336.

Dhamotharan, K., Tengs, T., Wessel, Ø., Braaen, S., Nyman, I.B., Hansen, E.F., Christiansen, D.H., Dahle, M.K., Rimstad, E. and Markussen, T. (2019). Evolution of the Piscine orthoreovirus Genome Linked to Emergence of Heart and Skeletal Muscle Inflammation in Farmed Atlantic Salmon (Salmo salar). Viruses, 11(5), p.465. Diserud, O. H., Hindar, K., Karlsson, S., Glover, K., and Skaala, Ø. 2020. Genetic impact of escaped farmed Atlantic salmon on wild salmon populations – revised status 2020. Norway: Report 1337. 55pp. Norwegian Institute for Nature Research. Trondheim, Norway: Report 1926. 84 pp.

https://brage.bibsys.no/xmlui/handle/11250/2435442

Gov.scot (2021). Seal licensing - gov.scot. [online] Available at:

<a href="https://www.gov.scot/collections/marine-licensing-seal-licensing/">https://www.gov.scot/collections/marine-licensing-seal-licensing/> [Accessed 12 October 2021].</a>

Dopazo, C.P. (2020). The Infectious Pancreatic Necrosis Virus (IPNV) and its Virulence Determinants: What is Known and What Should be Known. Pathogens, 9(2), p.94.

Draganovic, V., Jørgensen, S.E., Boom, R., Jonkers, J., Riesen, G. and van der Goot, A.J. (2013). Sustainability assessment of salmonid feed using energy, classical exergy and eco-exergy analysis. Ecological Indicators, 34, pp.277–289.

Drangsholt, T.M.K., Gjerde, B., Ødegård, J., Finne-Fridell, F., Evensen, Ø. and Bentsen, H.B. (2011). Quantitative genetics of disease resistance in vaccinated and unvaccinated Atlantic salmon (Salmo salar L.). Heredity, 107(5), pp.471–477. Eliasen, K., Danielsen, E., Johannesen, Á., Joensen, L.L. and Patursson, E.J. (2018).

The cleaning efficacy of lumpfish (Cyclopterus lumpus L.) in Faroese salmon ( Salmo salar L.) farming pens in relation to lumpfish size and seasonality. Aquaculture, 488, pp.61–65.

Ellingsen, H., Olaussen, J.O. and Utne, I.B. (2009). Environmental analysis of the Norwegian fishery and aquaculture industry—A preliminary study focusing on farmed salmon. Marine Policy, 33(3), pp.479–488.

Ernst, W., Doe, K., Cook, A., Burridge, L., Lalonde, B., Jackman, P., Aubé, J.G. and Page, F. (2014). Dispersion and toxicity to non-target crustaceans of azamethiphos and deltamethrin after sea lice treatments on farmed salmon, Salmo salar. Aquaculture, 424-425, pp.104–112.

Faust, E., Halvorsen, K.T., Andersen, P., Knutsen, H. and André, C. (2018). Cleaner fish escape salmon farms and hybridize with local wrasse populations. Royal Society Open Science, *5*(3), p.171752.

Figueroa, C., Bustos, P., Torrealba, D., Dixon, B., Soto, C., Conejeros, P. and Gallardo, J.A. (2017). Coinfection takes its toll: Sea lice override the protective effects of vaccination against a bacterial pathogen in Atlantic salmon. Scientific Reports, 7(1).

Findlay, C., Ripple, H., Coomber, F., Froud, K., Harries, O., van Geel, N., Calderan, S., Benjamins, S., Risch, D. and Wilson, B., 2018. Mapping widespread and increasing underwater noise pollution from acoustic deterrent devices. Marine Pollution Bulletin, 135, pp.1042-1050.

Finstad, B., Kroglund, F., Bjørn, P.A., Nilsen, R., Pettersen, K., Rosseland, B.O., Teien, H.-C. ., Nilsen, T.O., Stefansson, S.O., Salbu, B., Fiske, P. and Ebbesson, L.O.E. (2012). Salmon lice-induced mortality of Atlantic salmon postsmolts experiencing episodic acidification and recovery in freshwater. Aquaculture, 362-363, pp.193–199.

Finstad, B., Kroglund, F., Strand, R., Stefansson, S.O., Bjørn, P.A., Rosseland, B.O., Nilsen, T.O. and Salbu, B. (2007). Salmon lice or suboptimal water quality — Reasons for reduced postsmolt survival? Aquaculture, 273(2-3), pp.374–383. Fiskeridirektoratet (2021). Rømmingsstatistikk. [online] Fiskeridirektoratet. Available at: https://www.fiskeridir.no/Akvakultur/Tall-oganalyse/Roemmingsstatistikk.

Fjelldal, P.G., Hansen, T.J. and Karlsen, Ø. (2020). Effects of laboratory salmon louse infection on osmoregulation, growth and survival in Atlantic salmon. Conservation Physiology, 8(1).

Fjørtoft, H.B., Nilsen, F., Besnier, F., Stene, A., Tveten, A.-K., Bjørn, P.A., Aspehaug, V.T. and Glover, K.A. (2021). Losing the "arms race": multiresistant salmon lice are dispersed throughout the North Atlantic Ocean. Royal Society Open Science, 8(5), p.210265.

Ford, J.S., Pelletier, N.L., Ziegler, F., Scholz, A.J., Tyedmers, P.H., Sonesson, U., Kruse, S.A. and Silverman, H. (2012). Proposed Local Ecological Impact Categories and Indicators for Life Cycle Assessment of Aquaculture. Journal of Industrial Ecology, 16(2), pp.254–265.

Frantzen, M., Bytingsvik, J., Tassara, L., Reinardy, H.C., Refseth, G.H., Watts, E.J. and Evenset, A. (2020). Effects of the sea lice bath treatment pharmaceuticals hydrogen peroxide, azamethiphos and deltamethrin on egg-carrying shrimp (Pandalus borealis). Marine Environmental Research, 159, p.105007.

Gargan, P.G., Forde, G., Hazon, N., Russell, D.J.F. and Todd, C.D. (2012). Evidence for sea lice-induced marine mortality of Atlantic salmon (Salmo salar) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Canadian Journal of Fisheries and Aquatic Sciences, 69(2), pp.343–353.

Gargan, P., Karlsbakk, E., Coyne, J., Davies, C. and Roche, W. (2016). Sea lice (Lepeophtheirus salmonis and Caligus elongatus) infestation levels on sea trout (Salmo trutta L.) around the Irish Sea, an area without salmon aquaculture. ICES Journal of Marine Science, 73(9), pp.2395–2407.

Garseth, Å.H., Fritsvold, C., Svendsen, J.C., Bang Jensen, B. and Mikalsen, A.B. (2017a). Cardiomyopathy syndrome in Atlantic salmon Salmo salar L.: A review of the current state of knowledge. Journal of Fish Diseases, 41(1), pp.11–26.

Garseth, Å.H., Gjessing, M.C., Moldal, T. and Gjevre, A.G. (2017b). A survey of salmon gill poxvirus (SGPV) in wild salmonids in Norway. Journal of Fish Diseases, 41(1), pp.139–145.

Gebauer, P., Paschke, K., Vera, C., Toro, J.E., Pardo, M. and Urbina, M. (2017). Lethal and sub-lethal effects of commonly used anti-sea lice formulations on non-target crab Metacarcinus edwardsii larvae. Chemosphere, [online] 185, pp.1019–1029. Available at: https://www.sciencedirect.com/science/article/pii/S004565351731161X [Accessed 28 Oct. 2019].

Geitung, L., Oppedal, F., Stien, L.H., Dempster, T., Karlsbakk, E., Nola, V. and Wright, D.W. (2019). Snorkel sea-cage technology decreases salmon louse infestation by 75% in a full-cycle commercial test. International Journal for Parasitology, 49(11), pp.843–846.

Gentry, K., Bui, S., Oppedal, F. and Dempster, T. (2019). Sea lice prevention strategies affect cleaner fish delousing efficacy in commercial Atlantic salmon sea cages. Aquaculture Environment Interactions.

Gharbi, K., Matthews, L., Bron, J., Roberts, R., Tinch, A. and Stear, M. (2015). The control of sea lice in Atlantic salmon by selective breeding. Journal of The Royal Society Interface, 12(110), p.20150574.

Gilbey, J., Sampayo, J., Cauwelier, E., Malcolm, I., Millidine, K., Jackson, F. and Morris, D.J. (2021). A national assessment of the influence of farmed salmon escapes on the genetic integrity of wild Scottish Atlantic salmon populations. Marine Scotland Science.

Gjedrem, T. (2010). The first family-based breeding program in aquaculture. Reviews in Aquaculture, 2(1), pp.2–15.

Gjelland, K., Serra-Llinares, R., Hedger, R., Arechavala-Lopez, P., Nilsen, R., Finstad, B., Uglem, I., Skilbrei, O. and Bjørn, P. (2014). Effects of salmon lice infection on the behaviour of sea trout in the marine phase. Aquaculture Environment Interactions, 5(3), pp.221–233.

Gjessing, M.C., Krasnov, A., Timmerhaus, G., Brun, S., Afanasyev, S., Dale, O.B. and Dahle, M.K. (2020). The Atlantic Salmon Gill Transcriptome Response in a Natural Outbreak of Salmon Gill Pox Virus Infection Reveals New Biomarkers of Gill Pathology and Suppression of Mucosal Defense. Frontiers in Immunology, 11.

GLOBEFISH (2021). Lackluster ending to salmon market in 2020 | GLOBEFISH | Food and Agriculture Organization of the United Nations. [online] www.fao.org. Available at: https://www.fao.org/in-action/globefish/market-reports/resourcedetail/en/c/1416627/.

Glover, K.A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A.G.E. and Skaala, Ø. (2012). Three Decades of Farmed Escapees in the Wild: A Spatio-Temporal Analysis of Atlantic Salmon Population Genetic Structure throughout Norway. PLoS ONE, 7(8), p.e43129.

Glover, K.A., Solberg, M.F., Besnier, F. and Skaala, Ø. (2018). Cryptic introgression: evidence that selection and plasticity mask the full phenotypic potential of domesticated Atlantic salmon in the wild. Scientific Reports, 8(1).

Glover, K.A., Solberg, M.F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M.W., Hansen, M.M., Araki, H., Skaala, Ø. and Svåsand, T. (2017). Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. Fish and Fisheries, 18(5), pp.890–927.

Glover, K.A., Wennevik, V., Hindar, K., Skaala, Ø., Fiske, P., Solberg, M.F., Diserud, O.H., Svåsand, T., Karlsson, S., Andersen, L.B. and Grefsrud, E.S. (2020). The future looks like the past: Introgression of domesticated Atlantic salmon escapees in a risk assessment framework. Fish and Fisheries, 21(6), pp.1077–1091.

Glover, K., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M. and Skaala, Ø. (2013). Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14(1), p.74. Godwin, S.C., Krkosek, M., Reynolds, J.D. and Bateman, A.W. (2020a). Sea-louse abundance on salmon farms in relation to parasite-control policy and climate change. ICES Journal of Marine Science.

Godwin, S.C., Krkošek, M., Reynolds, J.D. and Bateman, A.W. (2020b). Bias in selfreported parasite data from the salmon farming industry. Ecological Applications. Götz, T. and Janik, V., 2014. Target-specific acoustic predator deterrence in the marine environment. Animal Conservation, 18(1), pp.102-111

Grøntvedt, R.N., Kristoffersen, A.B. and Jansen, P.A. (2018). Reduced exposure of farmed salmon to salmon louse (Lepeophtheirus salmonis L.) infestation by use of plankton nets: Estimating the shielding effect. Aquaculture, 495, pp.865–872. Gutierrez, A.P., Yáñez, J.M. and Davidson, W.S. (2016). Evidence of recent signatures of selection during domestication in an Atlantic salmon population. Marine Genomics, 26, pp.41–50.

Halttunen, E., Gjelland, K-Ø., Hamel, S., Serra-Llinares, R-M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., Johnsen, I.A., Asplin, L., Karlsen, Ø., Bjørn, P-A. and Finstad, B. (2017). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. Journal of Fish Diseases, 41(6), pp.953–967.

Halvorsen, K.T., Larsen, T., Sørdalen, T.K., Vøllestad, L.A., Knutsen, H. and Olsen, E.M. (2017). Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas. Marine Biology Research, 13(4), pp.359–369.

Halvorsen, K.T., Sørdalen, T.K., Durif, C., Knutsen, H., Olsen, E.M., Skiftesvik, A.B., Rustand, T.E., Bjelland, R.M. and Vøllestad, L.A. (2016). Male-biased sexual size dimorphism in the nest building corkwing wrasse (Symphodus melops): implications for a size regulated fishery. ICES Journal of Marine Science: Journal du Conseil, 73(10), pp.2586–2594.

Hannisdal, R., Nøstbakken, O.J., Hove, H., Madsen, L., Horsberg, T.E. and Lunestad, B.T. (2020). Anti-sea lice agents in Norwegian aquaculture; surveillance, treatment trends and possible implications for food safety. Aquaculture, 521, p.735044. Harte, A., Bowman, A., Salama, N. and Pert, C. (2017). Factors influencing the longterm dynamics of larval sea lice density at east and west coast locations in Scotland.

Diseases of Aquatic Organisms, 123(3), pp.181–192.

Heino, M., Svåsand, T., Wennevik, V. and Glover, K. (2015). Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquaculture Environment Interactions, 6(2), pp.185–190.

Helgesen, K.O., Romstad, H., Aaen, S.M. and Horsberg, T.E. (2015). First report of reduced sensitivity towards hydrogen peroxide found in the salmon louse Lepeophtheirus salmonis in Norway. Aquaculture Reports, 1, pp.37–42.

Helland, I., Uglem, I., Jansen, P., Diserud, O., Bjørn, P. and Finstad, B. (2015). Statistical and ecological challenges of monitoring parasitic salmon lice infestations in wild salmonid fish stocks. Aquaculture Environment Interactions, 7(3), pp.267– 280.

Higuera, G., Bastías, R., Tsertsvadze, G., Romero, J. and Espejo, R.T. (2013). Recently discovered Vibrio anguillarum phages can protect against experimentally induced vibriosis in Atlantic salmon, Salmo salar. Aquaculture, 392-395, pp.128– 133.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Foss, A., Vikingstad, E. and Elvegård, T.A. (2014). The use of lumpfish (Cyclopterus lumpus L.) to control sea lice (Lepeophtheirus salmonis Krøyer) infestations in intensively farmed Atlantic salmon (Salmo salar L.). Aquaculture, 424-425, pp.18–23.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E. and Elvegård, T.A. (2015). Feeding preferences of lumpfish (Cyclopterus lumpus L.) maintained in open net-pens with Atlantic salmon (Salmo salar L.). Aquaculture, 436, pp.47–51.

IPCC, 2021: Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [MassonDelmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press. In Press. Iversen, A., Asche, F., Hermansen, Ø. and Nystøyl, R. (2020). Production cost and competitiveness in major salmon farming countries 2003–2018. Aquaculture, 522, p.735089.

Jackson, D., Cotter, D., Newell, J., McEvoy, S., O'Donohoe, P., Kane, F., McDermott, T., Kelly, S. and Drumm, A. (2013). Impact ofLepeophtheirus salmonisinfestations on migrating Atlantic salmon, Salmo salar L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. Journal of Fish Diseases, [online] 36(3), pp.273–281. Available at: http://aquacomgroup.com/wordpress/wpcontent/uploads/2013/01/Jackson-et-al-2013-impact-of-lice-on-salmon-smolts.pdf. Jaramillo, D., Gardner, I.A., Stryhn, H., Burnley, H. and Larry Hammell, K. (2017). Bayesian latent class analysis of diagnostic sensitivity and specificity of tests for surveillance for bacterial kidney disease in Atlantic salmon Salmo salar. Aquaculture, 476, pp.86–93.

Jones, S., Bruno, D., Madsen, L. and Peeler, E. (2015). Disease management mitigates risk of pathogen transmission from maricultured salmonids. Aquaculture Environment Interactions, 6(2), pp.119–134.

Jones, S. R. M. (2019). Characterization of Piscirickettsia salmonis and salmonid rickettsial septicaemia to inform pathogen transfer risk assessments in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2019/020. v + 21 p.

Karlsen, C., Thorarinsson, R., Wallace, C., Salonius, K. and Midtlyng, P.J. (2017). Atlantic salmon winter-ulcer disease: Combining mortality and skin ulcer development as clinical efficacy criteria against Moritella viscosa infection. Aquaculture, 473, pp.538–544.

Karlsson, S., Diserud, O.H., Fiske, P. and Hindar, K. (2016). Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. ICES Journal of Marine Science, 73(10), pp.2488–2498.

Karreman, G., Klotins, K., Bebak, J., Gustafson, L., Osborn, A., Kebus, M.J., Innes, P. and Tiwari, A. (2015). Aquatic Animal Biosecurity: A Case Study of Bioexclusion of Viral Hemorrhagic Septicemia Virus in an Atlantic Salmon Hatchery. Journal of Applied Aquaculture, 27(3), pp.299–317.

Kawaguchi, S. and Nicol, S. (2020). Krill Fishery. In: G. Lovrich and M. Thiel, eds., Fisheries and Aquaculture: Volume 9. Oxford: Oxford University Press.

Keeley, N.B., Forrest, B.M. and Macleod, C.K. (2013). Novel observations of benthic enrichment in contrasting flow regimes with implications for marine farm monitoring and management. Marine Pollution Bulletin, 66(1-2), pp.105–116. Keeley, N.B., Macleod, C.K., Hopkins, G.A. and Forrest, B.M. (2014). Spatial and temporal dynamics in macrobenthos during recovery from salmon farm induced organic enrichment: When is recovery complete? Marine Pollution Bulletin, 80(1-2), pp.250–262.

Kent, A.J., Pert, C.C., Briers, R.A., Diele, K. and Rueckert, S. (2020). Increasing intensities of Anisakis simplex third-stage larvae (L3) in Atlantic salmon of coastal waters of Scotland. Parasites & Vectors, 13(1).

Kibenge, F.S. (2019). Emerging viruses in aquaculture. Current Opinion in Virology, 34, pp.97–103.

Klemme, I., Hyvärinen, P. and Karvonen, A. (2021). Cold water reduces the severity of parasite-inflicted damage: support for wintertime recuperation in aquatic hosts. Oecologia, 195(1), pp.155–161.

Kragesteen, T.J., Simonsen, K., Visser, A.W. and Andersen, K.H. (2019). Optimal salmon lice treatment threshold and tragedy of the commons in salmon farm networks. Aquaculture, 512, p.734329.

Kristoffersen, A.B., Qviller, L., Helgesen, K.O., Vollset, K.W., Viljugrein, H. and Jansen, P.A. (2018). Quantitative risk assessment of salmon louse-induced mortality of seaward-migrating post-smolt Atlantic salmon. Epidemics, 23, pp.19–33. Krkošek, M. (2017). Population biology of infectious diseases shared by wild and farmed fish. Canadian Journal of Fisheries and Aquatic Sciences, 74(4), pp.620–628. Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B. and Todd, C.D. (2013). Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences, [online] 280(1750), p.20122359. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3574446/. Lauringson, M., Nousiainen, I., Kahar, S., Burimski, O., Gross, R., Kaart, T. and Vasemägi, A. (2021). Climate change-driven disease in sympatric hosts: Temporal dynamics of parasite burden and proliferative kidney disease in wild brown trout and Atlantic salmon. Journal of Fish Diseases, 44(6), pp.689–699.

Long, A., Garver, K.A. and Jones, S.R.M. (2018). Differential Effects of Adult Salmon LiceLepeophtheirus salmonison Physiological Responses of Sockeye Salmon and Atlantic Salmon. Journal of Aquatic Animal Health, 31(1), pp.75–87.

Lovy, J., Piesik, P., Hershberger, P.K. and Garver, K.A. (2013). Experimental infection studies demonstrating Atlantic salmon as a host and reservoir of viral hemorrhagic septicemia virus type IVa with insights into pathology and host immunity. Veterinary Microbiology, 166(1-2), pp.91–101.

Madhun, A.S., Wennevik, V., Skilbrei, O.T., Karlsbakk, E., Skaala, Ø., Fiksdal, I.U., Meier, S., Tang, Y. and Glover, K.A. (2017). The ecological profile of Atlantic salmon escapees entering a river throughout an entire season: diverse in escape history and genetic background, but frequently virus-infected. ICES Journal of Marine Science, 74(5), pp.1371–1381.

Marine Scotland Directorate (2021). Diseases of wild and farmed Finfish. [online] www.gov.scot. Available at: https://www.gov.scot/publications/diseases-of-wild-and-farmed-finfish/.

Mc Dermott, T., D'Arcy, J., Kelly, S., Downes, J.K., Griffin, B., Kerr, R.F., O'Keeffe, D., O'Ceallachain, M., Lenighan, L., Scholz, F. and Ruane, N.M. (2021). Novel use of nanofiltered hyposaline water to control sea lice (Lepeophtheirus salmonis and Caligus elongatus) and amoebic gill disease, on a commercial Atlantic salmon (Salmo salar) farm. Aquaculture Reports, 20, p.100703.

McEwan, G.F., Groner, M.L., Burnett, D.L., Fast, M.D. and Revie, C.W. (2016). Managing aquatic parasites for reduced drug resistance: lessons from the land. Journal of The Royal Society Interface, 13(125), p.20160830.

McGinnity, P., Jennings, E., deEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K. and Cross, T. (2009). Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. Proceedings of the Royal Society B: Biological Sciences, [online] 276(1673), pp.3601–3610. Available at:

https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2817300/ [Accessed 9 Dec. 2019]. Mente, E., Martin, J.C., Tuck, I., Kormas, K.A., Begoña Santos, M., Bailey, N. and Pierce, G.J. (2010). Mesoscale effects of aquaculture installations on benthic and epibenthic communities in four Scottish sea lochs. Aquatic Living Resources, 23(3), pp.267–276.

Middlemas, S.J., Fryer, R.J., Tulett, D. and Armstrong, J.D. (2012). Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fisheries Management and Ecology, 20(1), pp.68–74.

Middlemas, S.J., Raffell, J.A., Hay, D.W., Hatton-Ellis, M. and Armstrong, J.D. (2010). Temporal and spatial patterns of sea lice levels on sea trout in western Scotland in relation to fish farm production cycles. Biology Letters, 6(4), pp.548–551.

Montes, R.M., Quiñones, R.A. and Gallardo-Escárate, C. (2022). Disentangling the effect of sea temperature and stocking density on sea louse abundance using wavelets in a highly infested salmon farming area. Aquaculture, 546, p.737246.

Moore, I., Dodd, J.A., Newton, M., Bean, C.W., Lindsay, I., Jarosz, P. and Adams, C.E. (2018). The influence of aquaculture unit proximity on the pattern of

Lepeophtheirus salmonis infection of anadromous Salmo trutta populations on the isle of Skye, Scotland. Journal of Fish Biology, 92(6), pp.1849–1865.

Mordecai, G.J., Miller, K.M., Bass, A.L., Bateman, A.W., Teffer, A.K., Caleta, J.M., Di Cicco, E., Schulze, A.D., Kaukinen, K.H., Li, S., Tabata, A., Jones, B.R., Ming, T.J. and Joy, J.B. (2021). Aquaculture mediates global transmission of a viral pathogen to wild salmon. Science Advances, 7(22).

Mørkøre, T., Moreno, H.M., Borderías, J., Larsson, T., Hellberg, H., Hatlen, B., Romarheim, O.H., Ruyter, B., Lazado, C.C., Jiménez-Guerrero, R., Bjerke, M.T., Benitez-Santana, T. and Krasnov, A. (2020). Dietary inclusion of Antarctic krill meal during the finishing feed period improves health and fillet quality of Atlantic salmon (Salmo salarL.). British Journal of Nutrition, 124(4), pp.418–431.

Morton, A., Routledge, R. and Krkosek, M. (2008). Sea Louse Infestation in Wild Juvenile Salmon and Pacific Herring Associated with Fish Farms off the East-Central Coast of Vancouver Island, British Columbia. North American Journal of Fisheries Management, 28(2), pp.523–532.

Morton, A., Routledge, R.D. and Williams, R. (2005). Temporal Patterns of Sea Louse Infestation on Wild Pacific Salmon in Relation to the Fallowing of Atlantic Salmon Farms. North American Journal of Fisheries Management, 25(3), pp.811– 821.

Morton, A., Routledge, R., Hrushowy, S., Kibenge, M. and Kibenge, F. (2017). The effect of exposure to farmed salmon on piscine orthoreovirus infection and fitness in wild Pacific salmon in British Columbia, Canada. PLOS ONE, 12(12), p.e0188793. Morton, A., Routledge, R., Hrushowy, S., Kibenge, M. and Kibenge, F. (2021). Correction: The effect of exposure to farmed salmon on piscine orthoreovirus infection and fitness in wild Pacific salmon in British Columbia, Canada. PLOS ONE, 16(3), p.e0248912.

Myhre Jensen, E., Horsberg, T.E., Sevatdal, S. and Helgesen, K.O. (2020). Trends in de-lousing of Norwegian farmed salmon from 2000–2019—Consumption of medicines, salmon louse resistance and non-medicinal control methods. PLOS ONE, 15(10), p.e0240894.

Naylor, R.L., Hardy, R.W., Bureau, D.P., Chiu, A., Elliott, M., Farrell, A.P., Forster, I., Gatlin, D.M., Goldburg, R.J., Hua, K. and Nichols, P.D. (2009). Feeding aquaculture in an era of finite resources. Proceedings of the National Academy of Sciences, [online] 106(36), pp.15103–15110. Available at:

https://www.pnas.org/content/106/36/15103.

Nekouei, O., Vanderstichel, R., Thakur, K., Arriagada, G., Patanasatienkul, T., Whittaker, P., Milligan, B., Stewardson, L. and Revie, C.W. (2018). Association between sea lice (Lepeophtheirus salmonis) infestation on Atlantic salmon farms and wild Pacific salmon in Muchalat Inlet, Canada. Scientific Reports, 8(1). Newton, R.W. and Little, D.C. (2017). Mapping the impacts of farmed Scottish salmon from a life cycle perspective. The International Journal of Life Cycle Assessment, 23(5), pp.1018–1029.

Nguyen, T.D., Crosbie, P.B.B., Nowak, B.F. and Bridle, A.R. (2018). The effects of inactivation methods of Yersinia ruckeri on the efficacy of single dip vaccination in Atlantic salmon (Salmo salar). Journal of Fish Diseases, 41(7), pp.1173–1176.

Nørstebø, S.F., Lotherington, L., Landsverk, M., Bjelland, A.M. and Sørum, H. (2018). Aliivibrio salmonicida requires O-antigen for virulence in Atlantic salmon (Salmo salar L.). Microbial Pathogenesis, 124, pp.322–331.

Northridge, S., Coram, A. & Gordon, J. (2013). Investigations on seal depredation at Scottish fish farms. Edinburgh: Scottish Government.

Nowlan, J.P., Britney, S.R., Lumsden, J.S. and Russell, S. (2021). Experimental Induction of Tenacibaculosis in Atlantic Salmon (Salmo salar L.) Using

Tenacibaculum maritimum, T. dicentrarchi, and T. finnmarkense. Pathogens, 10(11), p.1439.

Nylund, A., Brattespe, J., Plarre, H., Kambestad, M. and Karlsen, M. (2019). Wild and farmed salmon (Salmo salar) as reservoirs for infectious salmon anaemia virus, and the importance of horizontal- and vertical transmission. PLOS ONE, 14(4), p.e0215478.

Oh, E.S., Edgar, G.J., Kirkpatrick, J.B., Stuart-Smith, R.D. and Barrett, N.S. (2015). Broad-scale impacts of salmon farms on temperate macroalgal assemblages on rocky reefs. Marine Pollution Bulletin, 98(1-2), pp.201–209.

Olsen, R.E., Suontama, J., Langmyhr, E., Mundheim, H., Ringo, E., Melle, W., Malde, M.K. and Hemre, G.-I. . (2006). The replacement of fish meal with Antarctic krill, Euphausia superba in diets for Atlantic salmon, Salmo salar. Aquaculture Nutrition, 12(4), pp.280–290.

Olsen, R.L. and Hasan, M.R. (2012). A limited supply of fishmeal: Impact on future increases in global aquaculture production. Trends in Food Science & Technology, 27(2), pp.120–128.

Overton, K., Barrett, L., Oppedal, F., Kristiansen, T. and Dempster, T. (2019). Sea lice removal by cleaner fish in salmon aquaculture: a review of the evidence base. Aquaculture Environment Interactions.

Overton, K., Dempster, T., Oppedal, F., Kristiansen, T.S., Gismervik, K. and Stien, L.H. (2018). Salmon lice treatments and salmon mortality in Norwegian aquaculture: a review. Reviews in Aquaculture, 11(4), pp.1398–1417.

Page, F.H. and Burridge, L. (2014). Estimates of the effects of sea lice chemical therapeutants on non-target organisms associated with releases of therapeutants from tarped net-pens and well-boat bath treatments: a discussion.

Parsons, A.E., Escobar-Lux, R.H., Sævik, P.N., Samuelsen, O.B. and Agnalt, A.-L. (2020). The impact of anti-sea lice pesticides, azamethiphos and deltamethrin, on European lobster (Homarus gammarus) larvae in the Norwegian marine environment. Environmental Pollution, 264, p.114725.

Penston, M.J. and Davies, I.M. (2009). An assessment of salmon farms and wild salmonids as sources of Lepeophtheirus salmonis (Krøyer) copepodids in the water column in Loch Torridon, Scotland. Journal of fish diseases, [online] 32(1), pp.75–88. Available at: https://www.ncbi.nlm.nih.gov/pubmed/19245632.

Peters, L., Spatharis, S., Dario, M.A., Dwyer, T., Roca, I.J.T., Kintner, A., Kanstad-Hanssen, Ø., Llewellyn, M.S. and Praebel, K. (2018). Environmental DNA: A New Low-Cost Monitoring Tool for Pathogens in Salmonid Aquaculture. Frontiers in Microbiology, 9.

Philis, G., Ziegler, F., Gansel, L.C., Jansen, M.D., Gracey, E.O. and Stene, A. (2019). Comparing Life Cycle Assessment (LCA) of Salmonid Aquaculture Production Systems: Status and Perspectives. Sustainability, 11(9), p.2517.

Philis, G., Ziegler, F., Jansen, M.D., Gansel, L.C., Hornborg, S., Aas, G.H. and Stene, A. (2021). Quantifying environmental impacts of cleaner fish used as sea lice treatments in salmon aquaculture with life cycle assessment. Journal of Industrial Ecology.

Powell, A., Pooley, C., Scolamacchia, M. and de Leaniz, C.G. (2018). Review of lumpfish biology. In: J. Treasurer, ed., Cleaner Fish Biology and Aquaculture Applications. 5m Publishing.

Price, M.H.H., Proboszcz, S.L., Routledge, R.D., Gottesfeld, A.S., Orr, C. and Reynolds, J.D. (2011). Sea Louse Infection of Juvenile Sockeye Salmon in Relation to Marine Salmon Farms on Canada's West Coast. PLoS ONE, 6(2), p.e16851. Pulkkinen, K., Suomalainen, L.-R. ., Read, A.F., Ebert, D., Rintamäki, P. and Valtonen, E.T. (2009). Intensive fish farming and the evolution of pathogen virulence: the case of columnaris disease in Finland. Proceedings of the Royal Society B: Biological Sciences, 277(1681), pp.593–600.

Reed, T.E., Prodöhl, P., Hynes, R., Cross, T., Ferguson, A. and McGinnity, P. (2015a). Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. Heredity, 115(2), pp.173–184. Reed, T.E., Prodöhl, P., Hynes, R., Cross, T., Ferguson, A. and McGinnity, P. (2015b). Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. Heredity, 115(2), pp.173–184. Rimstad, E. and Markussen, T. (2020). Infectious salmon anaemia virus—molecular biology and pathogenesis of the infection. Journal of Applied Microbiology, 129(1), pp.85–97.

Salmon Scotland (2021). Scottish farmed salmon sector calls for action on predation. [online] www.salmonscotland.co.uk. Available at:

https://www.salmonscotland.co.uk/news/press-release/scottish-farmed-salmon-sector-calls-for-action-on-predation [Accessed 29 Nov. 2021].

Samsing, F., Rigby, M., Tengesdal, H.K., Taylor, R.S., Farias, D., Morrison, R.N., Godwin, S., Giles, C., Carson, J., English, C.J., Chong, R. and Wynne, J.W. (2020). Seawater transmission and infection dynamics of pilchard orthomyxovirus (POMV) in Atlantic salmon (Salmo salar). Journal of Fish Diseases, 44(1), pp.73–88. Satake, A. and Araki, H. (2011). Stocking of captive-bred fish can cause long-term population decline and gene pool replacement: predictions from a population dynamics model incorporating density-dependent mortality. Theoretical Ecology, 5(2), pp.283–296.

Schiermeier, Q. (2010). Ecologists fear Antarctic krill crisis. Nature, 467(7311), pp.15–15.

Scottishsalmon.co.uk. 2021. Scottish salmon sector sets out position on the use of acoustic deterrent devices. [online] Available at:

<https://www.scottishsalmon.co.uk/news/press-release/scottish-salmon-sector-setsout-position-on-the-use-of-acoustic-deterrent> [Accessed 12 October 2021].

Serra-Llinares, R., Bjørn, P., Finstad, B., Nilsen, R. and Asplin, L. (2016). Nearby farms are a source of lice for wild salmonids: a reply to Jansen et al. (2016). Aquaculture Environment Interactions, 8, pp.351–356.

Serra-Llinares, R., Bøhn, T., Karlsen, Ø., Nilsen, R., Freitas, C., Albretsen, J., Haraldstad, T., Thorstad, E., Elvik, K. and Bjørn, P. (2020). Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. Marine Ecology Progress Series, 635, pp.151–168.

Shea, D., Bateman, A., Li, S., Tabata, A., Schulze, A., Mordecai, G., Ogston, L., Volpe, J.P., Neil Frazer, L., Connors, B., Miller, K.M., Short, S. and Krkošek, M. (2020). Environmental DNA from multiple pathogens is elevated near active Atlantic salmon farms. Proceedings of the Royal Society B: Biological Sciences, 287(1937), p.20202010.

Shephard, S. and Gargan, P. (2017). Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environment Interactions, 9, pp.181–192.

Shephard, S. and Gargan, P. (2020). Wild Atlantic salmon exposed to sea lice from aquaculture show reduced marine survival and modified response to ocean climate. ICES Journal of Marine Science.

Shephard, S. and Gargan, P. (2021). System-specific salmon louse infestation thresholds for salmon farms to minimize impacts on wild sea trout populations. Aquaculture Environment Interactions, 13, pp.377–388.

Shephard, S., MacIntyre, C. and Gargan, P. (2016). Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. Aquaculture Environment Interactions, [online] 8, pp.597–610. Available at: https://www.int-res.com/articles/aei2016/8/q008p597.pdf.

Sherry, J. and Koester, J. (2020). Life Cycle Assessment of Aquaculture Stewardship Council Certified Atlantic Salmon (Salmo salar). Sustainability, 12(15), p.6079. Silva, C.B., Valente, L.M.P., Matos, E., Brandão, M. and Neto, B. (2017). Life cycle assessment of aquafeed ingredients. The International Journal of Life Cycle Assessment, 23(5), pp.995–1017.

Skaala, Ø., Besnier, F., Borgstrøm, R., Barlaup, B., Sørvik, A.G., Normann, E., Østebø, B.I., Hansen, M.M. and Glover, K.A. (2019). An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. Evolutionary Applications, 12(5), pp.1001–1016.

Skaala, Ø., Glover, Kevin A., Barlaup, Bjørn T., Svåsand, T., Besnier, F., Hansen, Michael M. and Borgstrøm, R. (2012). Performance of farmed, hybrid, and wild Atlantic salmon (Salmo salar) families in a natural river environment. Canadian Journal of Fisheries and Aquatic Sciences, 69(12), pp.1994–2006.

Skiftesvik, A.B., Blom, G., Agnalt, A.-L., Durif, C.M.F., Browman, H.I., Bjelland, R.M., Harkestad, L.S., Farestveit, E., Paulsen, O.I., Fauske, M., Havelin, T., Johnsen, K. and Mortensen, S. (2013). Wrasse (Labridae) as cleaner fish in salmonid aquaculture – The Hardangerfjord as a case study. Marine Biology Research, 10(3), pp.289–300.

Skilbrei, O. (2010). Reduced migratory performance of farmed Atlantic salmon post-smolts from a simulated escape during autumn. Aquaculture Environment Interactions, 1(2), pp.117–125.

Sprague, M., Dick, J.R. and Tocher, D.R. (2016). Impact of sustainable feeds on omega-3 long-chain fatty acid levels in farmed Atlantic salmon, 2006–2015. Scientific Reports, 6(1).

Starliper, C.E. (2011). Bacterial coldwater disease of fishes caused by Flavobacterium psychrophilum. Journal of Advanced Research, 2(2), pp.97–108.

Sundberg, L.-R., Ketola, T., Laanto, E., Kinnula, H., Bamford, J.K.H., Penttinen, R. and Mappes, J. (2016). Intensive aquaculture selects for increased virulence and interference competition in bacteria. Proceedings of the Royal Society B: Biological Sciences, 283(1826), p.20153069.

Sundt-Hansen, L., Huisman, J., Skoglund, H. and Hindar, K. (2015). Farmed Atlantic salmon Salmo salar L. parr may reduce early survival of wild fish. Journal of Fish Biology, 86(6), pp.1699–1712.

Susdorf, R., Salama, N., Todd, C., Hillman, R., Elsmere, P. and Lusseau, D. (2018). Context-dependent reduction in somatic condition of wild Atlantic salmon infested with sea lice. Marine Ecology Progress Series, 606, pp.91–104.

Sylvester, E.V.A., Wringe, B.F., Duffy, S.J., Hamilton, L.C., Fleming, I.A., Castellani, M., Bentzen, P. and Bradbury, I.R. (2019). Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. Evolutionary Applications, [online] 12(4), pp.705–717. Available at: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6439497/. Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, E., Kvamme, B.O., Boxaspen, K.K., Bjørn, P.A., Finstad, B., Madhun, A.S., Morton, H.C. and Svåsand, T. (2014). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, [online] 72(3), pp.997-1021. Available at: https://academic.oup.com/icesjms/article/72/3/997/686282. Tett, P., Benjamins, S., Black, K., Coulson, M., Davidson, K., Fernandes, T. F., Fox, C., Hart, M., Hicks, N., Hughes, A., Hunter, D. C., Nickell, T., Risch, D., Tocher, D., Vare, L., Verspoor, E., Wilding, T., Wilson, B., & Wittich, A. (2018). Review of the environmental impacts of salmon farming in Scotland. http://www.parliament.scot/parliamentarybusiness/CurrentCommittees/107588.asp Х Thorstad, E.B. & Finstad, B. (2018). Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout. NINA Report 1449: 1-22. Thorstad, E.B., Fleming, I.A., McGinnity, P., Soto, D., Wennevik, V. & Whoriskey, F. (2008). Incidence and impacts of escaped farmed Atlantic salmon Salmo salar in nature. NINA Special Report 36. 110 pp Thorstad, E., Todd, C., Uglem, I., Bjørn, P., Gargan, P., Vollset, K., Halttunen, E., Kålås, S., Berg, M. and Finstad, B. (2015). Effects of salmon lice Lepeophtheirus salmonis on wild sea trout Salmo trutta-a literature review. Aquaculture Environment Interactions, [online] 7(2), pp.91–113. Available at: https://www.salmon-trout.org/wp-content/uploads/2017/08/Thorstad-et-al-Effects-of-Salmon-Lice-on-Wild-Sea-Trout-Literature-Review.pdf. Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E. and Jackson, D. (2013). Salmon lice - impact on wild salmonids and salmon aquaculture. Journal of Fish Diseases, 36(3), pp.171–194. Torrissen, O., Olsen, R.E., Toresen, R., Hemre, G.I., Tacon, A.G.J., Asche, F., Hardy, R.W. and Lall, S. (2011). Atlantic Salmon (Salmo salar): The "Super-Chicken" of the Sea?. Reviews in Fisheries Science, 19(3), pp.257–278. Treasurer, J. (2018). An introduction to sea lice and the rise of cleaner fish. In: J. Treasurer, ed., Cleaner Fish Biology and Aquaculture Applications. 5m Publishing. Treasurer, J. and Feledi, T. (2014). The Physical Condition and Welfare of Five Species of Wild-caught Wrasse Stocked under Aquaculture Conditions and when Stocked in Atlantic Salmon, Salmo salar, Production Cages. Journal of the World Aquaculture Society, 45(2), pp.213–219.

Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C., Arrow, K.J., Barrett, S., Crépin, A.-S., Ehrlich, P.R., Gren, Å., Kautsky, N., Levin, S.A., Nyborg, K., Österblom, H., Polasky, S., Scheffer, M., Walker, B.H., Xepapadeas, T. and de Zeeuw, A. (2014). Does aquaculture add resilience to the global food system? Proceedings of the National Academy of Sciences, [online] 111(37), pp.13257–13263. Available at: https://www.pnas.org/content/111/37/13257.

Tucca, F., Moya, H., Pozo, K., Borghini, F., Focardi, S. and Barra, R. (2017). Occurrence of antiparasitic pesticides in sediments near salmon farms in the northern Chilean Patagonia. Marine Pollution Bulletin, [online] 115(1-2), pp.465– 468. Available at:

https://www.sciencedirect.com/science/article/pii/S0025326X16309614 [Accessed 28 Oct. 2019].

Uglem, I., Karlsen, Ø., Sanchez-Jerez, P. and Sæther, B. (2014). Impacts of wild fishes attracted to open-cage salmonid farms in Norway. Aquaculture Environment Interactions, 6(1), pp.91–103.

Uglem, I., Økland, F. and Rikardsen, A.H. (2012). Early marine survival and movements of escaped Atlantic salmonSalmo salarL. juveniles from a land-based smolt farm during autumn. Aquaculture Research, 44(12), pp.1824–1834.

Urbina, M.A., Cumillaf, J.P., Paschke, K. and Gebauer, P. (2019). Effects of pharmaceuticals used to treat salmon lice on non-target species: Evidence from a systematic review. Science of The Total Environment, 649, pp.1124–1136.

Van Geest, J.L., Burridge, L.E. and Kidd, K.A. (2014). Toxicity of two pyrethroidbased anti-sea lice pesticides, AlphaMax® and Excis®, to a marine amphipod in aqueous and sediment exposures. Aquaculture, 434, pp.233–240.

Verspoor, E., Knox, D. and Marshall, S. (2016). Assessment of interbreeding and introgression of farm genes into a small Scottish Atlantic salmonSalmo salarstock:ad hocsamples -ad hocresults? Journal of Fish Biology, 89(6), pp.2680–2696.

Verspoor, E., McGinnity, P., Bradbury, I., and Glebe, B. (2015). The potential direct and indirect genetic consequences for native Newfoundland Atlantic Salmon from interbreeding with European-origin farm escapes. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/030. viii + 36 p.

Villnäs, A., Perus, J. and Bonsdorff, E. (2011). Structural and functional shifts in zoobenthos induced by organic enrichment — Implications for community recovery potential. Journal of Sea Research, 65(1), pp.8–18.

Vollset, K., Barlaup, B., Mahlum, S., Bjørn, P. and Skilbrei, O. (2016). Estimating the temporal overlap between post-smolt migration of Atlantic salmon and salmon lice infestation pressure from fish farms. Aquaculture Environment Interactions, 8, pp.511–525.

Vollset, K.W. (2019). Parasite induced mortality is context dependent in Atlantic salmon: insights from an individual-based model. Scientific Reports, [online] 9(1), p.17377. Available at: https://www.nature.com/articles/s41598-019-53871-2? fbclid=IwAR3uPFsuqh-eh-

qpiFe80f1C1itZPmvoV4JhZ432EeK50tLZyzr47MCBeLk#Bib1 [Accessed 13 Jun. 2021].

Vollset, K.W., Krontveit, R.I., Jansen, P.A., Finstad, B., Barlaup, B.T., Skilbrei, O.T., Krkošek, M., Romunstad, P., Aunsmo, A., Jensen, A.J. and Dohoo, I. (2015). Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries, 17(3), pp.714–730.

Wacker, S., Aronsen, T., Karlsson, S., Ugedal, O., Diserud, O.H., Ulvan, E.M., Hindar, K. and Næsje, T.F. (2021). Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. Evolutionary Applications.

Wallace, I.S., McKay, P. and Murray, A.G. (2017). A historical review of the key bacterial and viral pathogens of Scottish wild fish. Journal of Fish Diseases, 40(12), pp.1741–1756.

Wells, A., Grierson, C.E., MacKenzie, M., Russon, I.J., Reinardy, H., Middlemiss, C., Bjørn, P.A., Finstad, B., Bonga, S.E.W., Todd, C.D. and Hazon, N. (2006). Physiological effects of simultaneous, abrupt seawater entry and sea lice (Lepeophtheirus salmonis) infestation of wild, sea-run brown trout (Salmo trutta) smolts. Canadian Journal of Fisheries and Aquatic Sciences, 63(12), pp.2809–2821. Wells, A., Grierson, C.E., Marshall, L., MacKenzie, M., Russon, I.J., Reinardy, H., Sivertsgård, R., Bjørn, P.A., Finstad, B., Wendelaar Bonga, S.E., Todd, C.D. and Hazon, N. (2007). Physiological consequences of "premature freshwater return" for wild sea-run brown trout (Salmo trutta) postsmolts infested with sea lice (Lepeophtheirus salmonis). Canadian Journal of Fisheries and Aquatic Sciences, 64(10), pp.1360–1369.

Wessel, Ø., Braaen, S., Alarcon, M., Haatveit, H., Roos, N., Markussen, T., Tengs, T., Dahle, M.K. and Rimstad, E. (2017). Infection with purified Piscine orthoreovirus demonstrates a causal relationship with heart and skeletal muscle inflammation in Atlantic salmon. PLOS ONE, 12(8), p.e0183781.

Wessel, Ø., Hansen, E.F., Dahle, M.K., Alarcon, M., Vatne, N.A., Nyman, I.B., Soleim, K.B., Dhamotharan, K., Timmerhaus, G., Markussen, T., Lund, M., Aanes, H., Devold, M., Inami, M., Løvoll, M. and Rimstad, E. (2020). Piscine Orthoreovirus-1 Isolates Differ in Their Ability to Induce Heart and Skeletal Muscle Inflammation in Atlantic Salmon (Salmo salar). Pathogens, 9(12), p.1050.

Whittaker, B.A., Consuegra, S. and Garcia de Leaniz, C. (2021). Personality profiling may help select better cleaner fish for sea-lice control in salmon farming. Applied Animal Behaviour Science, 243, p.105459.

Wringe, B.F., Jeffery, N.W., Stanley, R.R.E., Hamilton, L.C., Anderson, E.C., Fleming, I.A., Grant, C., Dempson, J.B., Veinott, G., Duffy, S.J. and Bradbury, I.R. (2018). Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Communications Biology, 1(1).

Ytrestøyl, T., Aas, T.S. and Åsgård, T. (2015). Utilisation of feed resources in production of Atlantic salmon (Salmo salar) in Norway. Aquaculture, [online] 448, pp.365–374. Available at:

https://www.sciencedirect.com/science/article/pii/S0044848615300624. Yuen, J.W., Dempster, T., Oppedal, F. and Hvas, M. (2019). Physiological performance of ballan wrasse (Labrus bergylta) at different temperatures and its implication for cleaner fish usage in salmon aquaculture. Biological Control, 135, pp.117–123.

Zalcman, E., Burroughs, A., Meyer, A., Hillman, A., Sadler, R., Madin, B., Mackenzie, C., Ward, M.P., Stevenson, M., Happold, J., Hutchison, J., Gallardo Lagno, A.L., Cameron, A. and Cowled, B. (2021). Sea lice infestation of salmonids in Chile between 2011 and 2017: Use of regulatory data to describe characteristics and identify risk factors. Aquaculture, 530, p.735752.