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

Summary

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, shortly 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 the world's population continues to grow so does the demand to produce sustainable food resources, with food demand by 2050 set to increase by 50%, and demand for animal-based foods by nearly 70% (World Resources Institute, 2018). Aquaculture is seen by many as an environmentally sustainable source of animal protein production, and companies are making record profits, opening new farms and farming more fish than ever before (Pandey et al., 2023). The United Nation's Food and Agriculture Organization (FAO) predicts that cultivated aquatic species will provide around 53% of the world's seafood supply by 2030 (Albrektsen et al., 2022). In 2023, a record 3 million tonnes of live weight salmon were grown (FAO, 2023).

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 between 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 infections, which can be transmitted through the free movement of water into wild fish populations. Atlantic salmon have demonstrably lower rates of survival as a result of sea lice infection pressure from farms. Sea trout and other salmonids also suffer infections because of salmon aquaculture. Due to increasing resistance to chemicals traditionally used to treat sea lice infestations, the salmon farming industry has in recent years focused on the use of cleaner fish to consume lice when stocked in salmon pen; however, serious concerns have emerged around the potential overharvesting of these species from the wild and the poor welfare they experience.

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 (Taranger et al., 2015) . The use of acoustic deterrent devices to exclude marine mammals that may damage salmon farm equipment also causes harm in many non-target cetaceans in parts of the world where they have not yet been banned.

The biggest impacts of salmon farming on the wider environment 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 constitute more than 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.

Escapes

It is an expected and accepted part of the aquaculture industry that farmed salmon frequently escape into the wider environment (Glover et al., 2020; Table 1). In both freshwater hatcheries and marine 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 12-29% of the true volume of escapes (Thorstad et al., 2008).

Table 1. Largest recorded Atlantic Salmon Escapes Globally (Navarro, 2019)

Company	**Year**	**Number of fish**	**Cause**
AquaChile Chile	2013	787,929	Damaged cages due to bad weather
Marine Harvest Chile	2018	680,000	Wind
Marine Harvest Norway	2005	496,000	Strong wind and electricity
Cypress Island Inc.	1997	369,000	Unknown
Meridian Salmon Farms	2011	336,470	High tides
Sjølaks Norway	2008	307,356	Unknown
Scottish Sea Farm Scotland	2000	258,000	Weather
Grieg Seafood Shetland Scotland	2002	238,420	Unknown
Australis Chile	2016	173,156	Displacement of modules due to strong underwater currents
SalMar Norway	2011	173,156	Unknown
Cooke Aquaculture United States	2017	150,000	Weather
Admiral Fish Farms Canada	2010	138,000	Net failure, manufacturing low mooring
Firda Sjøfarmer Norway	2013	122,914	Unknown
Huon Aquaculture Australia	2018	120,000	Weather
Firda Sjøfarmer Norway	2014	119,942	Unknown
Cermaq Chile	2017	115,703	Broken net due to major storm
Brilliant Fiskeoppdrett Norway	2009	115,000	Unknown
Cypress Island Inc.	1999	115,000	Unknown
Bakkafrost Faroe Islands	2017	109,515	Extreme weather conditions
Scan Am (later Cypress Island Inc.)	1996	107,000	Unknown

Scottish Sea Farm Scotland	1999	100,000	Weather
Sjøtroll Havbruk Norway	2008	100,000	Unknown

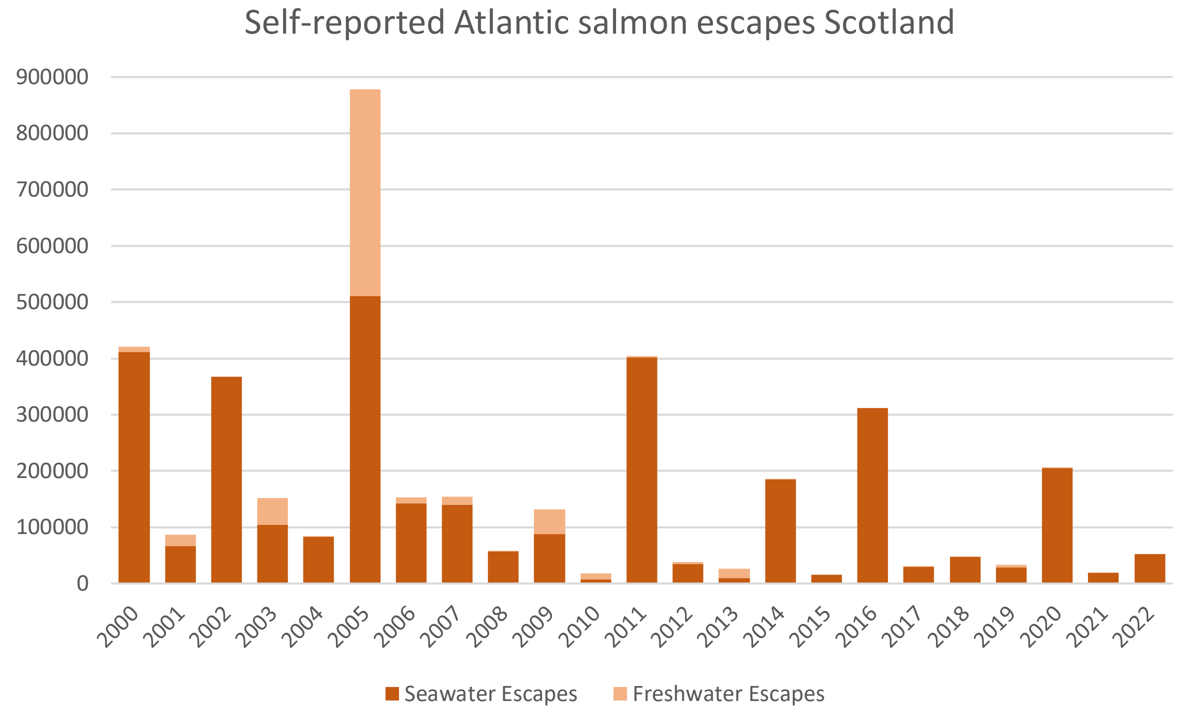

Figure 1. 20 years of escapes reported to the Scottish government (Scottish Fish Farm Production Surveys 2000-2022).

One study from Norway found that while reported 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 (figures 1 and 2). Planned expansion of marine aquaculture in Scotland from 200,000 tonnes of salmon produced in 2020 to 300,000 tonnes in 2030 is dependent on building outside of loch 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, in more exposed areas, at the mercy of increasingly extreme climate events.

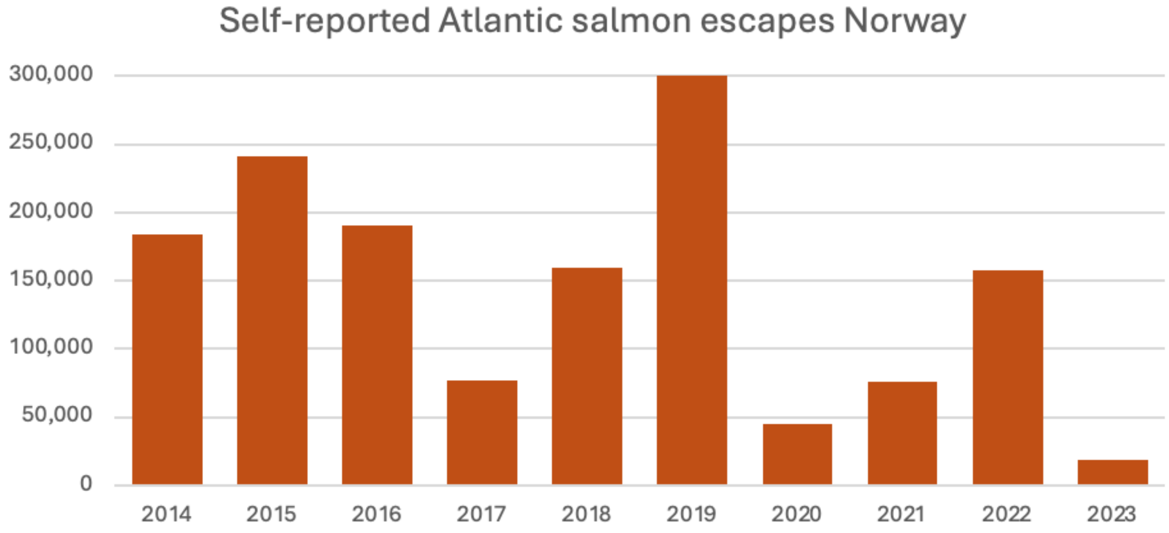

Figure 2. 10 years of escapes data reported to the Norwegian government (Fiskeridirektoratet, 2023)

Farmed Atlantic salmon are a domesticated strain of wild 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).

Following escape, Atlantic salmon disperse into the marine environment rapidly, making 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 hybridization.

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. Earlier escapes become better competitors with wild salmon than late escapes as they develop 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 farmed salmon have also been found to have more difficulty navigating river obstacles compared to their wild counterparts. Farmed to wild genetic introgression was found to be lower upstream of migration obstacles, and farmed salmon were observed to congregate below river barriers (Diserud et al., 2022). River barriers have been used in similar fashion to control the migration of invasive species upriver such as Chinese mitten crab and signal crayfish in the UK (Robinson et al., 2019; Sharov & Liebhold, 1998). However, farmed salmon which escaped earlier in their life cycle, and have spent a long time at sea, were more likely to overcome stream obstacles and be able to migrate to upstream spawning sites (Diserud et al., 2022). Therefore, river barriers would likely not be an effective solution to controlling potential hybridisation and already come with many other negative effects on wild salmon and wild fish populations, and are generally regarded as being environmentally degrading (O’Hanley et al., 2013; Połeć & Grzywna, 2023; Rolls et al., 2014).

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 and damage the nets trying to reach the fish (Callier et al., 2017). Escaped salmon frequently carry diseases at a higher 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 wild Atlantic salmon from farm escapes is the production of hybrids.

Hybridisation and outbreeding 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). Domestic salmon reared in the wild display a degree of phenotypic plasticity allowing them to develop into a morphology closer to a wild type that under farmed conditions, but still display genetically determined physical differences from wild populations including those from which the original source stock for domestic strain was derived (Glover et al., 2018; Gutierrez, Yáñez, and Davidson, 2016).

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 population of wild Atlantic salmon, this still represents a large proportion of the total Atlantic salmon population in the wild. 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. Madhun et al. (2023) erected fish traps on rivers with wild salmon populations between 2014 and 2018 to try and identify aquaculture escapees entering the river population for spawning. They found that more than half (59%) of escapees entering the river were mature; over half (55%) of recent escapees were mature, whilst among early escapees almost all (96%) were. Salmon who escape earlier in their lifecycle and survive to maturity thus have a greater chance of migrating to spawning grounds and reproducing with the local wild populations.

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). 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 a 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, Canada, 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).

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. (2021) 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).

Wild salmon are highly adapted to their specific environment and show a high level of genetic differentiation between populations in different rivers. Mixing of different wild populations is very uncommon (Gutierrez, Yáñez, and Davidson, 2016). This means recovering populations that have been lost is very challenging. Satake and Araki (2011) document how even captive salmon that are deliberately maintained to stock wild populations show considerably lower fitness than wild salmon. When the genetic diversity maintained in a population is lost, it cannot be regained. The second concern is for the genetic diversity of the entire species. The genetic divergence between wild populations is reducing because of shared genetic input from farmed populations, which reduces the capacity of the species to adapt to the growing challenges of climate change, habitat loss, and pollution (Glover et al., 2013). The proposed expansion of Atlantic salmon farming without significant changes to farming practices poses a serious threat not just to individual populations in close proximity to farms, but to the long-term survival of an already declining species.

Sea Lice

Effects of Sea Lice

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, once attached, all sea lice feed on the mucus, skin and blood of salmon. The most commonly occurring species in European 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.

Reduced farm salmon 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).

Alternative methods and technologies for salmon farming have been proposed and trialled to try and reduce the effects of sea lice. The two main alternatives are semi closed containment (SCC) and land-based systems. Both technologies are in their infancy and aim to provide separation between farmed salmon and open waters. They work by removing them from water bodies completely (land based) or by keeping salmon in enclosed floating cages with water exchange between the environment and the cage heavily filtered and restricted (SCC). SCC systems have been shown to show some benefits for reducing sea lice numbers to a 'certain degree' under specific circumstances, although there are other associated costs such as other microparasites and biofilms (Espmark et al., 2023). There needs to be more research into these technologies and their potential drawbacks, as currently independent studies (not linked to the aquaculture industry) are inconclusive as to the degree in which they reduce sea lice numbers, and also fish mortality. There are some documented improvements, but the significance of the results is not clear (Øvrebø et al., 2022). There is also concerns about the potential for fish escapes. Due to the more ridged structure of SCC systems any structural failure is likely to be catastrophic in comparison to open nets, as the whole structure will fail rather than smaller holes seen in many open net escapes.

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 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, and sea surface temperatures are currently at their highest in recorded history, with 2023-2024 being the hottest our oceans have been for each corresponding month of the year (Shephard and Gargan, 2020, Copernicus, 2024). Sea louse manipulation of the host salmon's immune system, which aids in successful parasitisation, also increases susceptibility to Infectious Salmon Anaemia (ISA) 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 co-infected 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 was correlated with sea lice numbers on nearby farms, with a stronger effect around farms with higher biomass (Penston and Davies, 2009). A recent study from Norway has established negative association of sea lice from salmon farms on recreational fishing catches of Atlantic Salmon (Larsen et al., 2024). In areas with high variability in sea-louse loads there is a consistent pattern where increased louse loads correspond to decreased wild salmon catches. Notably, when sea lice prevalence exceeds 0.1 lice per farmed fish, there is a 47% increase in the risk of below-average catches. This risk doubles when infestation levels surpass 0.2 lice per farmed fish. The findings suggest that the current threshold of 0.2 sea lice per farmed fish used in Norway is insufficient to avoid below-average recreational catches of salmon in areas surrounding salmon farms. A lower threshold of 0.1 is recommended to reduce this risk by 47% in the Norwegian study area. As salmon farming biomass increases, even adherence to this limit may be inadequate, suggesting the need for a total 'louse-emission limit'. Effective limits might be set at specific lice densities per square kilometre, with recommendations varying based on location (Larsen et al., 2024)

Some studies have suggested that sea lice-induced mortality is a significant but limited factor in the marine mortality of salmon, causing population level effects only in years when lice numbers are high and wild salmon struggling, but with warming seas and increasingly vulnerable wild populations these conditions will increase in frequency (Jackson et al., 2013). Analysis of a 26-year record from Ireland found that returns of one sea winter wild salmon were 50% lower in years following high lice levels on nearby farms (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 meta-analysis 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). 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.

However, other studies have questioned the effectiveness of treating out migrating salmon with antiparasitics (Vollset et al., 2023). There has been shown to be large variations in the amount of drug uptake via oral administration, and that the entire process of treating out migrating smolts reduces the chances of survival as the migrate out to sea (Lennox et al., 2020). Even more concerning, is that studies have shown that this form of treatment (usually in the form of administering emamectin benzoate) is becoming decreasingly effective in protecting wild salmon due to increasing levels of resistance among salmon lice adopted via evolution of the physiological system (Aaen et al., 2015; Lees et al., 2008).

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). Modelling sea lice transmission to wild salmon populations in Loch Linnhe in Scotland showed smaller smolts were more susceptible to sea lice, whilst larger, faster smolts were less at risk

(Moriarty et al., 2023). Atlantic Salmon smolt and post-smolt sizes have been shown to be in decline across the Atlantic as a result of anthropogenic and environmental pressures, which could make them more susceptible to sea lice infestation from aquaculture (Jutila et al., 2006; Kuparinen et al., 2009; Long et al., 2023).

Higher sea temperatures lead to much more rapid growth and transmission in sea lice as their development is temperature dependent. Seawater temperature has a major impact on the survival, reproduction rate and even infection success of sea lice. As seawater temperatures increase, sea lice can grow more rapidly, produce eggs more frequently and infect fish more readily (Hamre et al., 2019). In practice, this means that the number of sea lice emanating from open-net salmon farms can increase substantially as water temperatures increase. The number of days it takes sea lice eggs to hatch decreases substantially with increasing temperature; at 12°C, sea lice eggs only take 6.7 days to hatch, 2.7 times faster than at 6°C (16.8 days). Consequently, as temperatures rise, so to do the number of sea lice emanating from a single farm. Warmer temperatures can therefore increase the risk of potentially fatal infections in wild salmon and sea trout smolts.
At higher seawater temperatures, sea lice have better success attaching to, and infecting, salmon; one study found that fish infected at 10°C harboured twice as many copepodites as fish infected at 3°C (Dalvin et al., 2020).

This makes local and seasonal temperature 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 out-migrating post smolts from some Norwegian fjords (Vollset et al., 2016). One comparative study considering all possible contributors to sea lice infection in wild salmonids found that infection pressure from salmon farms was by far the most significant (Helland et al, 2015). Sea lice impact can be reduced by case-by-case modelling of wild salmon migration routes, in order to more strategically place salmon farms, track sea lice blooms, restricting farm biomass and/or control of numbers of ovigerous lice per fish, especially during smolt migration periods (Moriarty et al., 2023).

Recent studies however show that there is really only one solution to reducing the sea lice pressure on wild salmon populations; reducing the number of open net farmed salmon in wild salmon habitats. In Norway, Stige et al., (2024) found that the only measure which reduced salmon louse infestations to an acceptable level as defined by their regulatory ‘traffic light system’ (where salmon louse-induced mortality of migrating wild salmon post-smolts is evaluated against set targets) was to reduce the density of farmed salmonids in open cages. This could be accomplished by stocking open cages with larger fish to reduce exposure time or by reducing total fish numbers (Stige et al., 2024). Similar conclusions have been reached from studies in Canada. In the Discovery Islands region, the number of active salmon farms has reduced from eight to one between 2020 and 2022 (following a federal government order). During this time 1627 juvenile pink and chum salmon were examined for sea lice. The average number of sea lice per salmon declined by 96% during this period, and was almost entirely attributed to salmon farm removal (Routledge & Morton, 2023). No similar decline was witnessed during the same period in the Broughton Archipelago, only 50km away from the Discovery Islands despite 10 salmon farms being closed by 2022, but with 7 still remaining (Whitney, 2023). In fact, no other region wide area showed such a decline in Canada as the almost complete removal of salmon farms from the Discovery Islands, although in the case of the Broughton Archipelago, First Nations groups hope to close the remaining salmon farms after declining to provide written constent to Mowi and Cermaq to continue operating (Routledge & Morton, 2023; Whitney, 2023). It is clear from these case studies that the complete removal of open net salmon farms from wild salmon habitats is the most effective measure for protecting wild salmon from sea lice infestation.

Transmission to Sea Trout and Other Wild Fish

Sea lice, though often framed primarily as a problem for wild Atlantic salmon, also have 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.

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 years 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 (Bøhn et al., 2022). 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 that above the threshold of 13 mobile lice per fish weighing 19-70g, 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 more than 20,000 sea trout sampled across 94 lakes and rivers in Ireland, controlled for variable environmental conditions and background variation in population numbers and found that higher sea lice levels on sea trout were related both to proximity to aquaculture facilities and to higher temperature, which lead 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). A recent wider Norwegian study by Fiske et al. (2024) assessed the health of sea trout populations and anthropogenic pressures in coastal and riverine populations in Norway as a whole. 1251 water courses were assessed consisting of over 16,000 km of river and lakes. The human pressures assessed were hazardous substances (copper and nickel), culverts, sewage and runoff pollution, agriculture, acidification, hydropower production, water abstraction, habitat alterations, fishing exploitation and salmon lice from aquaculture. Salmon lice were found to be the greatest pressure facing sea trout populations, both in the number of watercourses they affected (80%), and greatest pressure in terms of river area (59.8%).

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 two-year salmon production cycles 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, when standardised sea lice counts are high on farms in April, there is a high probability of a below average sea trout run, 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 pressures of salmon aquaculture may lead to the establishment of exclusively freshwater populations of brown trout with lower overall genetic diversity (Thorstad et al., 2015 and Fiske et al., 2024). Similar selection pressure has been seen in declines in trout abundance in long and steep rivers due to the higher migration cost (Bohlin et al., 2001). If sea lice pressure becomes too great, we may see changes in genetic diversity and localised losses of anadromous populations and development of exclusively freshwater populations.

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.

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 studies have found that juvenile out-migrating 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 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 at 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; these are explained in table 2. But these are often based around self-reporting systems with audits from regulators. Godwin et al. (2020b) analysed self-reported 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 2) 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 (Hannisdal et al., 2020; McEwan et al., 2016).

Table 2. 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).

Norway	**Production Zones:** 13 zones using a traffic light-based system for sea lice. **Reporting:** Weekly reports on sea lice, sea temperature, treatments, number of cleaner fish, and sensitivity tests. **Control Measures:** • Maximum limit: 0.5 adult female lice (AF); 0.1 AF in spring during smolt migration. • Norwegian Food Safety Authorities (NFSA) actions: Coordinate de-lousing, introduce controls, order slaughtering and fallowing, reduce biomass for non-compliance. **Sensitivity Testing:** Managed by the Norwegian Veterinary Institute.
Chile	**Monitoring Program:** Introduced by Servicio Nacional de Pesca y Agricultura (Sernapesca) in 2007. **Sampling:** Weekly random sampling of 10 fish from four randomly selected cages. **Reporting:** Weekly lice counts, disease events, mortality, lab testing, treatments, and vaccinations.
Scotland	**Weekly Reporting:** Required since March 2021 to the Fish Health Inspectorate (FHI). **Action Levels:** • **If levels exceed 6.0 AF for <4 weeks and drop below 2.0 AF:** No action. • **If levels exceed 6.0 AF for <4 weeks but stay >2.0 AF:** o Advisory letter issued (1/2 breaches). o If continues for another 4 weeks: Second breach, enforcement notice issued. • **If levels exceed 6.0 AF for 6 weeks:** Enforcement notice issued. **Voluntary Code of Good Practice:** • 0.5 AFL per fish from February 1 to June 30. • 1.0 AFL per fish from July 1 to January 31.
Canada	**Sea Lice Counts:** Required in February for all pens. **Thresholds:** • Enter March-June period below 3.0 motile lice per fish. • From March to June: Report >3.0 motile lice to Department of Fisheries and Oceans (DFO) within 48 hours and take measures. • From July to January: Implement a sea lice management plan above 3.0 motile lice.

	Reporting: Pre and post-treatment counts, suspected treatment failures, monthly routine counts to DFO.
Ireland	**Monitoring:** Regular inspections by the Marine Institute. **Frequency:** 14 inspections per year per stock. **Publication:** Monthly results to stakeholders, annual public release. **Treatment Thresholds:** • Spring: 0.5 egg-bearing females per fish. • Rest of the year: 2.0 egg-bearing females per fish.
Faroe Islands	**Counting:** Every second week in summer, once a month in winter. **Limits:** • 1.5 egg-producing lice per salmon (set in 2017). • Reduced to 0.5 from June 1 to July 31 (2021). • 0.5 from May 1 to July 31 and 1.0 otherwise (2022 onward). **National Vet:** Can require treatments and coordinate between farms. **Reporting:** All treatments must be recorded and reported.
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" (Williamsburg Resolution, 2003)

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 2).

New preventative methods for reducing sea lice pressure are being developed, such as using plankton nets around the tops of cages which reduced infection pressure by up to 30%, or snorkels cages, which keep salmon below the surface other than a tube to access the surface allowing salmon to refill their swim bladders, and can reduce infection by 75%, but caused 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 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 that 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. In response to the declining effectiveness of chemical treatments, one approach that has been gaining popularity 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.

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.

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). Cleaner fish are also preferred as they are viewed as one of the most cost-effective methods of sea lice management. Cleaner fish ranked just below skirts and in-feed medicines in terms of cost-effectiveness on salmon farms in Scotland, at around £0.14 - £0.37 per fish unit of effectiveness (Boerlage et al., 2024). However, acquisition and deployment of cleaner fish in salmon farms requires careful consideration as managing these species introduces several new problems.

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 3.

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 more than 60 million cleaner fish are deployed a year. This figure does not consider stocking in Canada or Chile, two of the largest 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 wild 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. Farmed lumpfish have been found to show aggression to each other when raised in hatchery conditions resulting mainly in fin injuries, and when deployed into salmon aquaculture hatchery lumpfish are less robust their wild sourced counterparts (Boissonnot et al., 2023; Jonassen et al., 2018). When introducing farmed lumpfish into salmon cages, they exhibit increased stress from predatory sensory cues such as increased swimming activity, increased interspecies distance, and elevated plasma cortisol concentrations in comparison to using wild caught lumpfish (Staven et al., 2019). This is because they have not been habituated to interacting with other fish species and reduces their initial effectiveness and overall welfare.

Halvorsen et al., (2017) found that Corkwing wrasse were significantly older and larger inside marine protected areas in Norway than outside, 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've been harvested. Faust et al., (2018) found that genetically distinct goldsinny wrasse were escaping sea cages where they had been deployed and hybridizing with local populations.

Some recent studies have suggested that removing cleaner fish from the environment to be transferred into salmon farms may actually be doing more harm than good, rather than being a supposed 'sustainable' nature-based solution to sea lice control (Lennox et al., 2022). From the limited data available for Scandinavian wrasse, ecological modelling was performed on Atlantic salmon and trout by Lennox et al. (2022) to calculate the relative impact of lice when they are removed from the environment. Modelling found that wrasse fisheries may be a zero-sum game; removing wild cleaner fish, and the cleaning benefits they provide to wild fish, to use in salmon farms increases sea lice pressure on wild populations, whilst providing lesser benefits to farmed fish populations. They argue that cleaner fish should be left in their natural environment to fulfil their ecological niche, as even when rates of cleaning of wild salmonids is low, their efficiency of controlling lice populations in wild fish is far greater than if they were being used in aquaculture sites (Lennox et al., 2022).

Table 3. 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).

Cleaner fish	Biology and use in salmon farming
Cuckoo wrasse	Can live up to 17 years and reach 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).
Rock cook wrasse	Live up to 9 years and reach 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)
Goldsinny wrasse	Can live up to 14 (males) to 20 (females) years and reach 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)
Corkwing wrasse	Can live 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).
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. Two morphotypes with distinct life histories (may be subspecies, not confirmed). (Blanco Gonzalez and de Boer, 2017).
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).

Cleaner Fish Welfare

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). By 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 farmed salmon, 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 treatments, to try to combat rising sea lice numbers. A study in Norway showed that wrasse species have more significant impact reducing sea lice numbers than other species such as lumpfish, but this study was limited by cleaner fish being used in conjunction with thermal and chemical treatments, and the mortality rate and thus number of cleaner fish was not measured (Aldrin et al., 2023). 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. Mechanical delousing methods have been found to greatly increase lumpfish mortality in salmon farms, and therefore cleaner fish should not be kept in aquaculture cages when this is taking place. However (even though this is required under Norwegian aquaculture regulations) current recapture and sorting methods are not good enough. Fish farmers regularly fail to remove the whole population before delousing and the added stress of handling during removal further impounds stress and decreases lumpfish welfare (Aldrin et al., 2023). Until better capture methods are developed for lumpfish they should not be used when sea lice numbers increase, and delousing treatment is needed, due to the detrimental impacts on their welfare. 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 populations are suffering.

Whilst not directly used in salmon farming production, Bluestreak cleaner wrasse (a cousin of the wrasse species used as cleaner fish is salmon farms) has been shown to have the capacity of mirror self-recognition, similar to humans (Kohda et al., 2023). Fish were first shown the mirror image of themselves, then were marked and then presented with the mirror again where they would attempt to remove the mark from themselves, whilst repeatedly checking their reflection to ensure it was gone (Kohda et al., 2022). This display of mirror self-recognition has been interpreted by some scientists as evidence of self-awareness and raises uncomfortable questions as to the use of wrasse as an essentially expendable sea louse treatment for farmed salmon (which themselves are already kept in poor conditions). It also puts wrasse in the same category as humans, chimpanzees, orangutans, bottlenose dolphins and bonobos when it comes to displaying signs of cognitive self-awareness yet they are afforded a fraction of the protections (Lei, 2023). This is the first species of fish to have showed signs of self-recognition, and as our understanding of animal cognition advances, we may find that many other fish species have more advanced cognitive abilities than we previously thought, and we will need to rethink our current understanding of fish welfare.

Diseases

Salmon farms suffer not only from sea lice outbreaks, but from a host of other parasites and pathogens (table 4) 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).

Table 4. Common diseases of Atlantic salmon that are found in aquaculture environments due to movement of pathogens between aquaculture facilities and wild fish.

Disease	**Cause**	**Symptoms**	**Literature**
Amoebic gill disease	The causative agent is the protozoan parasite *Neoparamoeba perurans*. 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 *Flavobacterium psychrophilum.* 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 *Renibactterium salmoninarum* 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
Cardiomyopathy 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. It is still not well understood.	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
Diplostomum spathaceum	The causative agent is *Diplostomum spathaceum,* 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 if 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, zooplanktonic, harmful algal, and chemical/toxin). When the cause is not obvious gill disease is referred to as complex gill disease. When multiple causative agents are acting simultaneously it is multifactorial gill disease.	Gill diseases are usually associated with impaired respiratory function from damage to the gills, and often mortality.	(Boerlage et al., 2020)
Gill Pox Virus	The causative agent is a large DNA virus that infects Atlantic salmon gills.	Causes damage to the gills which leads to a high mortality and lasting damage in fish that recover.	(Gjessing et al., 2020)
Gyrodactylus Salaris	The small parasite *Gyrodactylus salaris* 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	(Wessel et al., 2020; Wessel et al., 2017)

		lesions on and inflammation of the heart, and necrosis of the red skeletal muscle.	
Infectious Haematopoietic 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 world. It can be transmitted horizontally in fresh and saltwater, through waste and in dead bodies, and vertically. It is highly infectious.	Mortality occurs predominantly in juvenile stages, recently including post-smolts. All age groups and both freshwater and marine environments can sustain infection. It is often present asymptomatically. Causes abdominal swelling and internal pancreatic necrosis, and infected groups can suffer 80-90% mortality.	(Dopazo, 2020) *and* Marine Scotland Directorate
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-HPR0 and the virulent ISAV-HPRΔ. ISAV-HPR0 is widespread in farmed salmon. ISVA-HPRΔ causes severe anaemia, haemorrhage in internal organs, ascites, darkening of the liver. The development of ISAV-HPR0 into ISVA-HPRΔ 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/ Piscirickettsiosis	The bacterium *Piscicickettsia salmonis* 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 oomycetes which are related to Chromista, chromophyte algae, and other Protista, not the fungi to which they are often compared. *Saprolegnia parasitica* 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
Tenacibaculosis/ yellow mouth/ mouth rot	Tenacibaculosis is caused by members of the flavobacteriaceae family, notably *Tenacibaculum maritimum, T. dicentrarchi* and *T. finnmerkense*. It	Causes erosion and haemorrhaging of the mouth, development of yellow plaques around	(Nowlan et al., 2021) *and*

	affects multiple marine species including Atlantic salmon and is, responsible for considerable aquaculture losses. There is no vaccine, it is treated with antibiotics.	the mouth, ulcerative skin lesions, frayed fins, tail rot.	Marine Scotland Directorate
Vibrosis	Vibrosis is caused by bacteria in the genus Vibrio, mostly commonly by *Listonella (Vibrio) anguillarum* 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 *Allivibro salmonicida*, and many other *Vibrio*s have been linked to fish diseases. An effective vaccine is widely used but does not prevent all outbreaks. 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
Winter ulcer disease	Caused by *Moritella viscosa* among others. An effective vaccination against *M. viscosa* 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)

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 situated near each other. 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 2017 observational study suggests it to be 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. Though transmission could not be confirmed they 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 for viable pathogens, shedding large quantities 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). eDNA has already been used successfully to detect emerging sea lice infestations autonomously from remote water monitoring sites (Krolicka et al., 2022). In regards to using eDNA to detect pathogens numerous recent studies have shown proof of concept for use in and around salmon farms, although as of yet there is limited actual field work showing disease spread, although this may soon change now a number of relevant methodologies have been created (Amarasiri et al., 2021; Shea et al., 2022; Sieber et al., 2024)

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 seven-year study found aquaculture conditions facilitated a shift towards high virulence at both short and long-time 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 (Pulkkien et al., 2009). 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. 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 will be very challenging to predict.

Organic and Nutrient Enrichment of the Benthos

One of the consistent interactions that open net salmon farming has with the environment around it 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.

A large scale study monitoring the benthic environment at a regional level in Norway at 759 salmon farms was conducted between 2016 and 2022, consisting of over 2480 different reports (Wang & Olsen, 2024). In concluded that the main controls on benthic enrichment were water depth, current velocity, maximum allowable biomass density and length of farm’s production cycle. Therefore, optimal biomass levels, production cycle arrangement, and farming practices should differ depending on specific environmental factors. The most severe environmental degradation was found to occur between summer and autumn periods, where maximal feeding rates were highest. Seafloor ecosystem recovery was possible, although recovery rates diminished depending on the existing time the environment had been under nutrient pressure.

Oh et al., (2015) found impacts of nutrient input on the benthic community extended on average 100-400m from farms. In a study on Scottish sea lochs, Mente et al., (2010) found no effect after 2000m from farms. However, 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, although 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.

Current environmental management frameworks in aquaculture mainly consider the nutrient enrichment potential of inshore sites. However, the industry is looking to unlock growth potential from open ocean sites which brings a host of new problems. With fish farms located in such environments, the potential for nutrient dispersal across a wider area could be significant (Elvines et al., 2024). Most investigations into the spatial dispersion of waste from fish farming have been performed in low energy hydrodynamic systems. Under these conditions waste readily accumulates making it easy to detect and measure in sediments immediately surrounding the aquaculture site. However, relatively few studies have been performed in high energy systems (more wave action, higher biologically productive environments) where organic material is more readily degraded, eroded or consumed by organisms (Elvines et al., 2024). One study which attempted to study this using fatty acid tracers at a dynamic costal site in Norway found that waste was dispersed up to 1100m, 500m further than the extent of clear organic enrichment of sediments observed in a concurrent study (Woodcock et al., 2019). There is also concern that climate warming could lead to greater waste dispersal as storm events and average wave heights have been found to be increasing across the globe (Allan & Komar, 2000; Bertin et al., 2013; Komar & Allan, 2008). Furthermore, there is growing evidence that in more dispersive locations epibenthic communities can have higher assimilative capacity than soft sediment fauna when exposed to low levels of waste (Keeley et al., 2020; McMullin, 2020; McMullin et al., 2021). Therefore, biochemical indicators such as fatty acids or stable isotopes may become important tools to identify environmental assimilation of waste over more dispersive sites and mixed habitats which the aquaculture industry are looking to expand into (Elvines et al., 2024). 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 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. Even at a much lower concentration, azamethiphos 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 (Parsons et 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 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. A recent study of Canadian salmon farm sediments in the Atlantic found the presence of anti-sea lice drugs and antibiotics were found in high concentrations within 200m of cages, and in lower concentrations up to 1.5 km away (Kingsbury et al., 2023). Multi-drug presence combined with organic and/or metal enrichment show the potential for cumulative effects from chemical cocktails to pollute the benthic environment from salmon farming.

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 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).

Non-lethal management techniques include the use of net tensioning, seal blinds, and acoustic deterrent devices (ADDs), also known as acoustic harassment devices (AHDs). 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). 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). In August 2022 Environmental Standards Scotland effectively banned the use of ADDs, although they will still be permitted if they are compliant with the Habitats Regulations and the Aquaculture Code of Practice which requires them to either obtain any relevant consents or to demonstrate that their use will not harm marine mammals (Hunter, 2022).

Sustainability

The impacts of salmon farming on the immediate environment are one component of a much larger picture of wider environmental impact by the industry. 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 globalization 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 CO_2 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 meta-analysis 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 2.8 million tonnes of live weight salmon in 2023, the quantity of marine ingredients included as fish meal and fish oil in salmon feed has fallen (Iversen et al., 2020; FAO, 2023). 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). There is a limited global supply of fishmeal and oil; most species harvested for its product 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). Various metrics are used to assess the sustainability of salmon feed options 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).

A better use of wild fish used as aquafeeds would be redirecting them towards direct human consumption instead. A recent study by Willer et al., (2024) found that directly consuming fish traditionally used as aquafeed such as anchovies and mackerel would provide a more nutrient rich food than the salmon they are used to feed, as only 1-49% of essential dietary minerals and fatty acids available in wild fish are retained in farmed salmon (Willer et al., 2022). Atlantic salmon currently uses 60% of global fish oil and 23% of global fishmeal used in aquaculture, yet salmon production is only 4.5% of global aquaculture yield (Willer et al., 2022). Reallocating wild fish used for aquaculture to human consumption would increase seafood production and allow the by-products to still be retained for further use, thus maximising nutrient utilisation of marine resources (Willer et al., 2024). Removing wild-caught fish from salmonid production could leave 3.7 Mt fish in the sea while increasing global seafood production by 6.1 Mt (Willer et al., 2022)

Any supplement used for fishmeal or fish oil must still have a similar nutrient profile to adequately meet the needs of growing salmon. The most promising alternative feed ingredients and sources for feed production have been outlined by Albrektsen et al., (2022) and (Wickins, 1988):

- low-trophic species (mesopelagic fish, zooplankton, polychaetes, macroalgae and crustaceans)
- novel microbial ingredients (bacteria, yeast and microalgae)
- insects (black soldier fly, yellow meal worm and crickets)
- animal by-products (poultry meal, meat and bone meal, blood meal and hydrolysed feather meal)
- by-products from other commercial productions (trimmings and blood)
- Plant material (grasses, legumes, cereals and oil-bearing seeds or cakes)

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 (by-product fish meal and fish oil, by-product 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. The method of accounting can have a large impact on the results of a LCA; however, this demonstrates that by-product substitutions are not the silver bullet they are often presented to be. One feeding trial found that the feeding salmon an insect/algal based fish feed compared to marine caught wild feed also resulted in a greater environmental impact (Goglio et al., 2022). However, this was attributed mainly to inefficient production pathways used in insect/algae production, soybean protein concentrates and rapeseed oil.

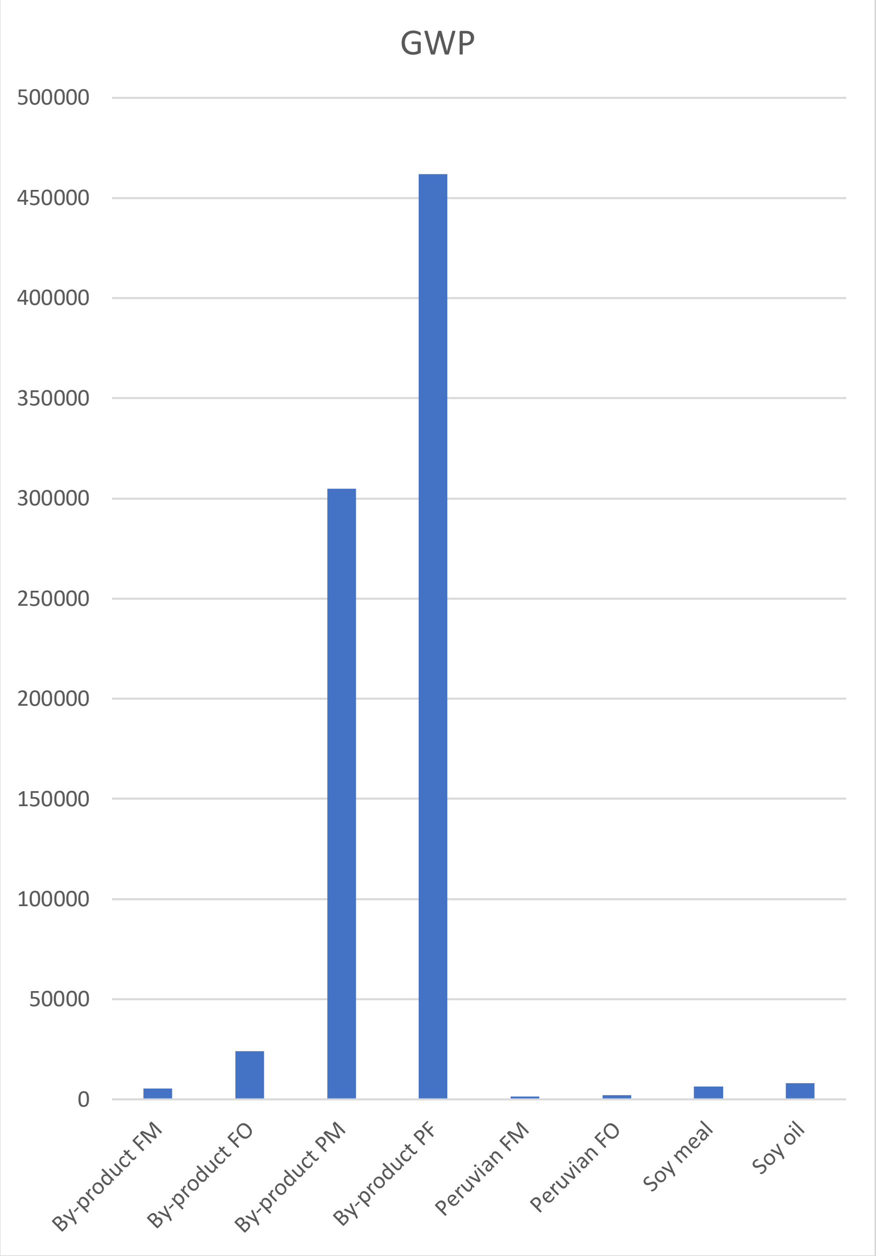

Figure 3. The global warming potential (GWP) in kg CO2 eq per 1t of ingredients commonly used in salmon feed including fish meal (FM), fish oil (FP), poultry meal (PM) and poultry fat (PF). Data based on life cycle analysis by Silva et al., (2017).

One industry response to sustainability challenges posed by using wild caught fish in farmed salmon feed has been to increase the proportion of plant material used. 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 significant processing to produce a feed from plants with a high enough fat and protein content, and low enough fibre and anti-nutrient content that salmon grow and develop normally. Most of the plant-based 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.

Advances in processing soy, wheat and rapeseed to make digestible plant-based protein and fat sources for salmon feed have improved sustainability of salmon relative to other food sources. 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.

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. Due to the higher chitin content a 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.

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.

Conclusions

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

- Escapes cause acute threat from competition during large scale escapes. The escapes outnumber wild populations.
- Escapes cause chronic threat from outbreeding depression and hybridization. Wild salmon are 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 from *C. elongatus* 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 cruelty without proven benefit.
- Diseases are a chronic threat from exposure to greater infection pressure from a greater number of diseases.
- Diseases cause acute threats from 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 threats from deposition of nutrients and organic matter changing benthic community structures and the spread of antiparasitic drugs killing (commercially important) crustaceans.
- Wider environment suffers chronic threats 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 food and for which 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 these threats. 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 epizootic and disease outbreaks, with harms that are then easily spread to the environment, will always have a cost for wild fish and their wider environment.

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