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Salmon Lice: The Environmental History of a Troubled Relationship

In October 2013, the Sea Lice Research Centre at the University of Bergen received a batch of *Lepeoptheirus salmonis* (Krøyer) from a site in Northwestern Norway.¹ A salmon producer had shipped the ectoparasites to the wet laboratory at the Centre, fearing that the local lice population had developed reduced sensitivity to a chemical known as hydrogen peroxide (H_2O_2) . The farmer wanted the Centre to experimentally verify observations made by the salmon pen by performing a controlled bioassay that compared the sampled strains against strains verified as H_2O_2 -sensitive.

L. salmonis belongs among the copepods, a diverse subclass of crustaceans. The salmon louse is considered a menace to salmon welfare as it is specialized to feed on blood and mucus. When large numbers of lice feed on the same fish, its protective skin is weakened, which can

¹In this text, "salmon louse" refers to *L. salmonis*. The term "sea lice" is occasionally confused with the thimble jellyfish (*Linuche unguiculata*), causing "sea bather's eruption." Colloquially, "sea lice" also refers to related copepod parasites infecting a variety of fish, such as *Caligus elongatus* ("skottelus," or "fiskelus"), *Caligus curtus* ("torskelus"), and *Caligus rogercresseyii*.

cause secondary infections and problems with osmoregulation. High lice levels are also considered a threat to migrating stocks of wild salmon in the fjords where these farms are located. Furthermore, salmon lice management is extremely costly, and many interventions have unwanted environmental consequences. In 2018, it was estimated that the price tag for treatments and prevention in Norway was around 5.2 billion NOK, making *L. salmonis* a contentious topic in public debates about the future of salmon farming.

In 2013, chemical delousing with hydrogen peroxide was one of the few tools sea farmers had at their disposal for emergency interventions when lice levels rose above the legal threshold of 0.5 adult female lice per fish on average. To the public, this substance is better known for its industrial applications as an antiseptic and bleaching agent, than its role in food production. Salmons are treated with this highly oxidative compound by being pumped into enclosed tanks in specially designed well boats from their marine pens. Here, the fish swims around in a $H₂O₂$ solution for a few minutes depending on the strength of the liquid, causing lice to fall off, before the fish is pumped back into its enclosure. Although the operation is costly, labor-intensive, and stressful for the fish, it would indeed be grave news for the industry, and for future fish health work, if the parasite had become resistant to yet another compound. Unfortunately, the bioassays performed by scientists at the Centre confirmed the farmer's suspicions about hydrogen peroxide resistance, and their conclusions were later independently verified by other researchers. There was conclusive evidence that natural selection had, again, caught up with human attempts at controlling the lice population, which now resisted another treatment in a rapidly depleting arsenal of therapeutics. While deeply concerning for salmon farmers, this was also an exciting opportunity for the biologists to better understand the genetics of drug resistance. The lice that arrived in the laboratory were therefore used to cultivate a new H_2O_2 -resistant strain of salmon lice for experimental uses.

This chapter tells the story of how salmon lice ended up as an object of intense experimental scrutiny in the laboratory. To make sense of this we must situate the parasite within the environmental history of salmon domestication, and how the management of *L. salmonis* emerged as a

most critical challenge. In what follows, I first conceptualize parasitism, domestication, and the great acceleration of marine domestication. I then narrate some of the early experiments in Norwegian aquaculture, and the trajectory of its fish-farming industry in the postwar period. We then turn to the context of fish health biology as a subject for scientific management in Norway, and how salmon lice emerged as a critical issue for the farming industry. I end by outlining how scientific fish health management contributes to a deeply coevolutionary, interspecies process of domestication that takes place both in the sea and in the lab.

Parasites

The 6th Edition of the *Oxford Dictionary of Biology* defines parasitism as "an association in which one organism (*the parasite*) lives on (*exoparasitism*), or in (*endoparasitism*), the body of another (the *host*), from which it obtains its nutrients" (Martin & Hine, [2008\)](#page-37-0). This non-mutual, antagonistic relationship is a driving force in the evolution of life's diversity on Earth. Estimates of biodiversity suggest that more of the planet's existing organisms have a parasitic, rather than non-parasitic, lifestyle.

Biological anthropologists consider parasitism to be a central feature in our species' past, and phylogenetic studies of primate parasitism provide indirect evidence to track the evolutionary and behavioral history of our hominem ancestors (Perry, [2014\)](#page-39-0). Humanity most likely acquired most of our parasite interlocutors from close primate relatives, or from animals frequently accompanying us. But the agricultural revolution likely influenced the coevolution between humans and our parasite guests more than any proceeding event. Every domestication project undertaken by humans since has entailed the creation and maintenance of new precarious relationships with parasites. Globalization has further contributed to the exchange of parasites between people and places, with the Columbian Exchange being the most familiar example. The colonization of the Americas involved massive movements of parasitic organisms from east to west (McNeill, [2003\)](#page-38-0). With increased mobility today, parasites frequently become our fellow travelers.

Husbandry changed human lifestyles in fundamental ways, introducing unparalleled proximity to animals, with ample opportunities for transmission of animal infections to human bodies, a process called *zoonosis*. Today, we are afflicted by hundreds of parasitic species, not counting behavioral parasites, commensals like rats, obligate parasites without metabolism (viruses), and bacteria. These range from relatively innocent everyday endoparasites, like the nematode helminth pinworm (*Enterobius vermicularis*) which is widespread in nursery schools around the world, to more mischievous creatures. One is the human botfly *Dermatobia hominis*, whose nauseating effects on human bodies can be seen in many YouTube videos. Not to mention the four species from the microscopic, malaria-causing *Plasmodium*-genus, and exoparasitic arachnids, such as ticks, carriers of Lyme disease. History also tells us that our primordial relationship with parasites has even affected the rise and fall of world empires (McNeill, [1976\)](#page-38-1).

Here it is useful to draw a distinction between parasites that directly interferes with our bodies, neutral parasites that cause little nuisance, and those giving us trouble by infecting *other* species under our care, and whose welfare we are held morally accountable for. All domestication projects, including the taming of fish, inevitably means coping with parasitic interlocutors of some kind. Given that this is a story about the latter of these relationships, we will not be concerned with parasites that fulfil their energetic and reproductive requirements by tapping directly into human bodies. Rather, this is an account of parasitism "by proxy." It concerns the unforeseen challenges that arose when we attempted to master the Atlantic salmon along with its parasitic interlocutors, and how modern bioscience, with its potential to domesticate other life forms in the laboratory, was enrolled to solve a major problem with one of our most prized farm animals.

Domesticating Fish

What does it mean to say that a fish is domesticated? In her widely celebrated *The Natural History of Domesticated Animals*, Julie Clutton-Brock recalls Francis Galton's historical summary of "man's domination

and manipulation of the animal kingdom" [\(1999:](#page-36-0) 15–16). Writing in 1865, Galton offered six conditions for any species to qualify as "domesticable." First, young animals of the species must survive when reared away from the parents. Secondly, the animal must be adaptable to a dominance hierarchy that is compatible with human co-existence. Third, the animal must not be adapted for instant flight, so that it may feed and breed in confinement. Fourth, the animal must be useful for its human domesticators. Fifth, the animal must breed freely in captivity. Galton's sixth and final condition bundles several social traits: the animal must possess a reasonable temper and versatile feeding habits, prefer the company of conspecifics, and be amenable to human communication. Galton's list forcefully demonstrates that domestication, a process our species has been engaged in for over millennia (well over thirty thousand years in the case of dogs), is a profoundly biocultural process.

Although the inhabitants of Norway have intervened in salmonid life histories for hundreds of years, much older fish domesticates can be found in world history. In a survey of the existing archeological evidence, Nash suggests that Egyptians in the New Kingdom reared tilapia, a paraphyletic tribe of *Cichlidae*, in cultivation around 2500 BC, perhaps earlier (Nash, [2010\)](#page-38-2). Chinese common carp culture, a major fraction of farmed fish today, dates to at least 2070 BC. Although Egyptian practices might precede Chinese carp production, others suggest this was a rudimentary form of "proto-aquaculture" since tilapia may not primarily have been used as a food source (Beveridge & Little, [2002\)](#page-36-1). Other ancient precursors include pond culture with ceremonial and commercial functions for Sumerian temples, dating back to 2500 BC. Roman fish culture, known as *vivariae piscinae*, developed from Egyptian and Assyrian practices. European cultivation of freshwater fish, such as carp, can be traced back to at least thirteenth-century France (Hoffman, [1995\)](#page-37-1).

When do human intervention by feeding, hatching of fertilized eggs, and enhancement of fish habitats constitute domestication proper? The deep history of fish domestication is contentious. Balon suggests that fish, like other animals, should fulfill five criteria to qualify as fully domesticated [\(2004\)](#page-35-0). The fish must be valued and purposively kept, and breeding must be subject to human control. It must also display different

behaviors and phenotypic variations not found among wild conspecifics. Finally, the fish should not be able to survive without human intervention. Most cultured fish do not fulfil the fourth and fifth criteria, meaning that not even a purportedly "ancient" species like the Chinese carp qualify as true domesticates (ibid.: 4). Balon's conclusion is therefore that besides the common carp (*Cyprinus carpio*), only guppies (*Carassius auratus*) and neon tetra (*Paracheirodon innesi*) of modern aquarium culture are fully domesticated, arguably making "exploited captives" a more fitting term for encultured fish (ibid.: 21).

Although these conceptual distinctions offer clarity about the natural and cultural history of aquaculture, I remain agnostic about the value of defining strict criteria for qualifying salmon and other marine animals as *truly* domesticated. In a pragmatic spirit, I therefore frame salmon as "domesticated" in this book, seeing this as a dynamic process of mutual interaction and coordination between humans, cultured salmon, and parasites, unfolding over evolutionary time. This recognizes Darwin's key insight that the attributes and boundaries of species are never fixed essences. As with modern, enculturated humans, a wealth of selection pressures acts on the biology of farmed salmon, and the emergent outcomes of these interspecies dynamics cannot always be attributed to human intentions. As Lien has argued, telling "co-species histories" like that of salmon domestication through an anthropocentric master frame of human control is problematic when dealing with complex, nonlinear human-environment systems [\(2015:](#page-37-2) 3). She suggests that rather than redefining or sharpening our definition of domestication, we should recognize that we are dealing with a perpetual process of interspecies interactions, better understood in terms like mutuality, uncertainty, and tinkering. As we shall see, the industrial adventure of Norwegian salmon farming is also a co-species story about the unintentional proliferation of parasites.

The Great Acceleration of Marine Domestication

London, 1883. Although the first signs of a pending impoverishment in marine fisheries were appearing, overfishing was not yet an immediate concern. It certainly did not stop visitors from around the world to convene for the International Fisheries Exhibition. Here, those with a vested interest in marine resources could marvel at the latest technologies for harvesting the oceans. Among the spectacles people could admire were also state-of-the-art systems to enculture fish. However, many prominent intellectuals, the notable Thomas Huxley included, considered farming the seas to be a waste of time. After all, oceanic fisheries knew no limits at this point (Nash, [2010:](#page-38-2) 70). The prediction that aquaculture would potentially outgrow the outputs of conventional fisheries about a century later would strike the audience at the Exhibition as delusional.

Aquaculture takes place both in freshwater on land, and in salty oceans. While there has been a doubling of production every ten years for the past five decades, the growth of domesticated aquatic species first became a planetary force of reckoning in the 1980s, as production of a limited number of species greatly intensified (McNeill, [2001\)](#page-37-3). This trajectory coincided with the overexploitation of conventional fisheries which, although once considered virtually inexhaustible, are now producing near their maximum sustainable capacity (Naylor & Burke, [2005\)](#page-38-3). Shrimp aquaculture offers a telling example of this story. Its growth has been so rapid that it serves as a proxy for coastal zone development in a collection of statistical trends showcasing the "Great Acceleration" of major Earth-systems in the Anthropocene, a geological epoch recognizing humanity's planetary impact (Steffen et al., [2015\)](#page-39-1).

In their *State of World Fisheries and Aquaculture*, the FAO report that aquaculture continues to grow faster than any other sector of food production, although the growth rate is slower than in the 1990s [\(2019\)](#page-36-2). In 2018, the share of aquaculture in the global production of capture fisheries and aquaculture, reached 46.8%, a profound growth from 25.7% in the year 2000. Some researchers even project that "the development of aquaculture is bound to replace fisheries as animal husbandry

replaced hunting on land" (Duarte et al., [2007:](#page-36-3) 383). Two millennia ago, humans domesticated roughly 90% of the total number of currently domesticized terrestrial species, with a modest 3% increase since the Industrial Revolution. In comparison, large-scale aquaculture is knowledge and technology intensive, and coincides with the industrial age. 97% of all aquatic species currently domesticated were cultivated after the twentieth century began, with over 100 new species being domesticized in the past two decades. This rate is approximately a hundred times faster than for terrestrial species, and aquaculture has seen greater success when considering the fraction of known species under domestication.

Due to slow growth, long lifespans, specialized diets, and unsuitable behavioral traits, few remaining terrestrial species have the potential for domestication. Many marine species, however, have evolutionary affordances that makes them salient, as they can be bred for greater yield, with shorter generation times than terrestrial domesticates. Many fish, for example, have low levels of parental investment in their offspring after eggs have hatched. Additionally, there is a variety of taxa and species to domesticate, adapted to a broader range of habitats. New species are therefore brought under human stewardship each year, with estimates suggesting that a new marine species now require around ten years of intensive research to be commercially exploitable. Given the significant challenges faced by land-based operations, such as competition for limited resources like territory and freshwater, forecasts predict that coastal and offshore mariculture will expand the most in coming decades (Gentry et al., [2017\)](#page-36-4).

Salmon Farming and Salmon Lice

In Norway, where farming of high-value anadromous salmonid finfish has dominated, there have been heated public disputes about the costs of aquaculture. Sticking points include the potentially negative effects of salmon aquaculture on wild salmon stocks; disputes with conventional fisheries over coastal zone management; environmental pollutants and the challenge of sustainable feed production; and concerns about fish welfare (Aasetre & Vik, [2013;](#page-35-1) Lien, [2015;](#page-37-2) Rosenberg, [2008;](#page-39-2) Torrissen

et al., [2013\)](#page-39-3). Disputes about the great acceleration of salmon aquaculture hinge on fundamental disagreements about the past and future distribution of environmental costs. Some believe diversification of domesticated marine species represents a positive contribution by ensuring heterogeneity in habitat and resource consumption compared to other kinds of husbandry (Duarte et al., [2009\)](#page-36-5). Others argue that raising carnivorous finfish like salmonids, which consume nutrients that could be refined for human consumption, is akin to raising "tigers of the sea" (Naylor & Burke, [2005\)](#page-38-3). Other again, see feed resources as well-managed, and argues that farmed salmon utilizes plant and animal resources so efficiently that it should be positively framed as a "super-chicken of the sea", given the increased global demand for animal protein (Torrissen et al., [2011\)](#page-39-4).

On the assumption that Peak Oil is imminent before long, industrial fish farming in Norway has been rhetorically framed as the "New Oil" a pillar of the future economy of an expansive, oil-fueled welfare state. In one event, the Norwegian prime minister described salmon farming as "the Norwegian IKEA"; applying the frame of a successful industrial adventure based on mass-produced commodities to highlight its potential (NTB, [2015\)](#page-38-4). Others have framed salmon as "the Norwegian Tesla"; a luxury, high-tech food product, that disrupts conventional food production (Berge, [2014\)](#page-35-2). Given that increased levels of affluence have led to an increased protein demand, farmed salmon is also regularly framed as a contributor to the planet's food supply. Critics, however, counter that Norwegian salmon is a luxury commodity mainly targeting the affluent middle class. In this view, the expansion of aquaculture should prioritize more sustainable species, requiring less technological scaffolding and operating at a lower level in the food chain.

However, fish health problems caused by parasitic infections are arguably the most pressing challenge for Norwegian salmon aquaculture today. From a human health perspective, domestication of new aquatic species is relatively harmless compared to novel terrestrial animals; there are few concerns over potential zoonosis from aquatic animals due to the evolutionary distance that separates humans and aquatic organisms. But these new human–animal relationships present major challenges with

respect to the management of parasites in livestock production. Parasitic organisms threaten the welfare of animals in human custody, and parasites may also act as vectors for other pathogens. With the intensification of aquaculture, there is also a rise in the level of parasite infections, accompanied by increased expenditures on infection management and prophylaxis (Shinn et al., [2015\)](#page-39-5). Although many kinds of pathogens have proven troublesome for the development of salmon aquaculture, the crustacean ectoparasite *Lepeoptheirus salmonis* has been an unrivalled cost driver. Anti-lice interventions, which require labor-intensive monitoring, prevention, and treatment have become exorbitant. Bath treatments with hydrogen peroxide, for example, involve high-risk operations with well boats, chemicals, manpower, and heavy machinery at sea.

Medicinal feeds, like SLICE, are simple to administer, but costly and vulnerable to evolutionary adaptations for reduced sensitivity. Cleaner fish (wrasse and lump suckers), which are added to pens to eat lice from fish, must be tended and cared for on their own terms, and an entire professional field of cleaner-fish services has emerged as market demands for new solutions have soared. Many mechanical delousing options are also available: from simple external physical shields ("skirts") that protect pens from free-floating lice in the water stream, to high-tech equipment like truck-sized mechanical devices that removes lice using lukewarm water, as well as laser-based automated delousing machines. Rotational fallowing of farming sites is also costly and time-consuming. Estimates suggest that around 10% of production costs are now allocated to mediating this parasitic relationship, and costs are rising.

While lice have become entangled with every imaginable aspect of salmon domestication in recent years, the parasite was historically seen as a quality hallmark on wild salmon. Since lice are not well-adapted to freshwater, the presence of lice suggested that a salmon specimen had recently come upriver from the ocean to spawn. A Danish-Norwegian bishop and naturalist, Erik Pontoppidan (1698–1763), provided one of the first accounts (see Berland & Margolis, [1983\)](#page-35-3): "great schools of salmon moving from the sea into fresh water, partly to refresh themselves, and partly to rid themselves by rubbing and washing in the swift currents and waterfalls, of a kind of greenish vermin called 'Laxe-Luus,' attached between the fins, plaguing it in the heat of spring." *L. salmonis* was scientifically described by the zoologist Henrik Nikolai Krøyer in 1837. Although known to cause damage if present in great numbers, salmon lice were not considered a major pest on wild fish before the dawn of salmon aquaculture. With highly host-specific preferences, the parasite is specialized to exploit salmonids. Since these are non-schooling fish out at sea, any potential host specimens would be few and far between. But when higher densities of salmon farms became commonplace along the Norwegian coastline in the 1970s, the availability of host salmonids changed fundamentally. The parasite became more abundant, and antiparasitic interventions of farmers changed its population dynamics.

Ectoparasites on fish face a range of challenges. As other parasites, they must locate a host, attach, stay in place over time, acquire nutrients, and reproduce. Parasitic lifecycles are complex, and understanding their developmental pathways is central for coping with parasitic relationships. Salmon lice belong to the copepods, a group of small crustaceans found in most aquatic habitats and is currently believed to have an eight-stage life cycle. The first three life stages, known as nauplius I, II, and the copepodid-stage, are planktonic, and spent searching for a host in the sea. During the third stage, the parasite, now roughly 0.7 mm long, infects salmonid fish. The five subsequent life stages are spent in a parasitic relationship with the host. During the fourth and fifth life stages, the parasite attaches to fish by employing a protein filament, and in the remaining three stages (preadult I, II, and as a fully adult lice) the parasite moves about on the host's surface, inflicting damage on the fish by feeding on mucus and blood. Female specimens produce egg-strings containing several hundred eggs at a rapid pace. At 10 °C it generally takes a female around 50 days to mature from an egg into an adult specimen (40 days for males). Sexually dimorphic, adult males average around 5–6 mm, and females between 8 and 18 mm. At this point, the parasite may cause skin wounds, thereby exposing the fish to bacterial and fungal infections. These lesions may, in turn, disturb the osmotic salt balance of the fish, and if the infection pressure become sufficient, the stress caused by pathogen loads may cause weight loss, reduced health and death.

L. salmonis has become a recurring matter of concern in public debates about the future of salmon farming, although the effects of this negative media coverage on market demand have likely been negligible (Liu et al., [2016\)](#page-37-4). Some frames in these arguments reflect the normative expansion of our moral circle to include non-humans like farmed fish, including health and welfare concerns (Lund et al., [2007\)](#page-37-5). Does the fish suffer, and what is an acceptable amount of suffering in livestock production? Other frames question the sustainability of using chemotherapeutants against pathogens and their side effects on marine ecosystems (Aasetre & Vik, [2013\)](#page-35-1). Yet other conservation-laden frames emphasize the impact of lice on wild salmon due to the densities of current stocks of farmed salmon. Since the number of wild salmonids that migrate upriver along the Norwegian coast annually is minuscule in comparison with the millions of captive fish in pens, these frames highlight farms as pathogen reservoirs that can devastate wild stocks.

All these frames make assertions about how the costs of lice should be allocated. Consequentially, public debates about lice have become polarized around the question of how environmental externalities ought to be handled. Therefore, they also engender different solutions. Technooptimistic and economizing frames, stressing the economic costs of lice as an unresolved, but a tractable problem, draws other implications for regulatory management than risk frames that conceptualizes lice as an environmental concern, or an animal welfare issue. Despite disagreements over the solutions, there is consensus across different frames that the "lice-problem" must be solved to realize the potential of a blue, post-oil national economy.

Early Experiments in Norwegian Aquaculture

To understand how lice profoundly shaped Norwegian salmon aquaculture, and became an intriguing object of experimental science, we must look at the origins of salmon farming. Where land-based animal husbandry could draw on thousands of years of cumulative knowledge, those who brought this newcomer to the farm had to start from scratch.

Atlantic salmon (*Salmo salar*) and trout (*Salmo trutto*) were prized resources along the Norwegian coastline and rivers, and were traded as smoked, cured, or freshly iced. Humans have long affected fish populations unintentionally, through fishery-driven selection pressures for the evolution of early sexual maturation and other life-history characteristics. In the case of salmonids, intentional interventions in their river lives began in 1853, after a royal decree by the Danish king in a period of dispute about rights and entitlement to river fisheries. The Norwegian ichthyologist Halvor H. Rasch (1805–1883) led the first hatchery efforts, practicing what we today recognize as applied biological research on the process of stroking fish for gametes and fertilizing the ova with sperm (Solhaug, [1976:](#page-39-6) 548). By fertilizing and caring for the eggs until hatching, and rearing the resulting alevins, fish fry could be transplanted to enrich watersheds.

In his work *On the Artificial Propagation of Fish*, Rasch outlined new methods and identified several challenges in hatching and transplanting of freshwater fish, like the sensitive period from fertilization to the first feed uptake, which remain a critical bottleneck in salmon farming today. Rasch's vision was not purely scientific, although he won considerable recognition for his work, including a gold medal from the International Exposition in Paris 1867. He strongly believed that fish culture had unrealized commercial potential, by increasing important yields of anadromous fish species (Møller & Haaland, [2014a\)](#page-38-5). With his assistant, Marius G. Hetting, who became Norway's first fisheries inspector in 1868, Rasch promoted hatcheries to boost freshwater fisheries, and proposed regulatory measures to prevent overharvesting. While small-scale hatching efforts were practiced in Norway before Rasch and Hetting started touting its benefits, they successfully mobilized political support for experimental research on large-scale rearing of fish in both freshwater and seawater, where salmon and trout were known to grow quickly.

Others saw the potential in the artificial breeding of fish. Attuned to international trends, Rasch acquired knowledge from hatcheries abroad, such as in Scotland and France, at a time when naturalists across the continent saw potential in fish culture as a method to increase fisheries outputs by releasing fry into the oceans for sea ranching (Nash, [2010\)](#page-38-2).

Rasch was inspired by a Dane by the name of Heinz Kolding, who argued for the economic value of hatcheries in a letter to Norwegian authorities in 1851, the year when the first national salmon law (*Lakseloven*) came into effect. But despite valiant efforts by its advocates, large-scale pond culture in Norway was commercially unsuccessful at first. Among the Scandinavian countries, only Denmark developed a significant industry with organized feed provisioning and a sales organization. This loss of momentum could be ascribed to a variety of biological and technical problems. One tremendous challenge that any cultivation project must cope with is the problem of parasite-induced disease. The dynamics are relatively simple, as the main idea behind aquaculture is to confine large volumes of fish in a relatively small space. But high fish densities tend to intensify pathogen virulence and worsen disease outbreaks, in ways that are notoriously hard to mitigate. Without preventive measures and pharmaceutical intervention, populations of fish reared together are endangered by an assortment of microbes.

The nineteenth-century farmers who experimented with pond culture experienced the debilitating effects of these pathogens, and due to production challenges related to poor feed uptake and slow growth, pond culture eventually went dormant around the 1880s. This fiasco paved the way for imports of Danish roe and fry from allegedly superior disease-resistant Californian rainbow trout (*Oncorhynchus mykiss*), roughly two decades later (Møller & Haaland, [2014a\)](#page-38-5). Initiating a period known as the "rainbow fever," several new trout facilities were established with the hope of making good money around 1906 and 1907. But the fever passed, as these experiments with trout failed to meet expectations, possibly due to a lack of basic understanding of fish behavior, reproductive biology, nutrition, and disease. After these scattered attempts, Norwegian pond farming entered a period of stasis lasting throughout the Second World War.

While most fish-farming efforts failed to mature into a large-scale commercial success in the late nineteenth century, it nonetheless appears that the many experiments in pond culture across Europe provided key technological scaffolding that was instrumental for scaling up this niche half a century later (Nash, [2010:](#page-38-2) 80). In this period, marine

biology expanded as a scientific discipline, and new professional organizations and infrastructures dedicated to pursuing knowledge about aquatic ecosystems were created. For example, many hatchery laboratories established in Norway and elsewhere on the continent, under the auspice of Rasch and his likeminded peers, were gradually converted into facilities for marine biological science.

From Rural Sideline to Industrial Production

In the wake of the war, commercial pond culture again saw a revival, as a few faithful entrepreneurs started tinkering with the practice, once more by modelling the pattern of Danish trout farming. Some of these individuals became instrumental in turning Norwegian fish culture from a marginal sideline, basically an outgrowth of the composite subsistence strategy known as the "fisher-farmer" (*fiskerbonde*), into a massive commercial and technological success.

In 1962, there were only twenty to thirty active small-scale farms, when excluding those preoccupied with hatching and rearing fish for watershed management (Møller & Haaland, [2014b:](#page-38-6) 57). Producing an estimated thousand metric tons in 1969, their total output was commercially insignificant. While Norwegian farmers were endowed with suitable terrain and plenty of freshwater for their ponds, they were in the periphery of major continental markets. Furthermore, the produce was a pale, portion-sized trout of variable quality, in low demand both domestically and abroad.

Two radical shifts in farming practices in the late 1960s and early 1970s were pivotal for subsequent developments (Berge, [2000\)](#page-35-4). The first critical turning point was the decision to move the anadromous fish from freshwater to marine habitat, to deal with disease, slow growth, and poor feed uptake. The second transformation came when farmers switched from trout to Atlantic salmon, a species fetching much higher market value.

Past efforts to enculturate trout and salmon in saltwater had failed, but in the rural town of Sykkylven on the northwestern coast of Norway, two industrious brothers named Karstein and Olav Vik built a productive

experimental facility where they demonstrated the feasibility of saltwater farming. Taking inspiration from Denmark and determined to learn from past failures, this architect and farmer systematically studied critical bottlenecks, including salinity tolerance, feed uptake, and feeding regimens. Their first achievement was to establish brood fish that survived after spawning. Another breakthrough came when they demonstrated that rainbow trout and later, salmon, could be easily acclimatized to life in saltwater *polls* (enclosed inlets and creeks), even thriving in these environments. In 1959, the brothers placed young salmon in wooden floating cages and reared them to maturity over a three-year period. This story of success spread along the coast and stimulated new efforts at fish culture by industrious risk-takers. Two prominent examples were the owners of Mowi, a company that began raising salmon in saltwater polls on the island Sotra outside of Bergen, and the Grøndtvedt-brothers, based on the island Hitra. Many of these innovators saw great difficulties in acquiring wild roe from salmon fishermen, who reasonably considered farmed fish as competition to their own business. However, by the late 1960s, the demand for smolt had grown so large that hatcheries dedicated to smolt production were established outside of Bergen, which increased the availability of younglings to farmers (Nash, [2010:](#page-38-2) 123).

While freshwater cultivators could draw on the accumulated knowledge from pond culture and watershed management, the trailblazers who moved trout and salmon into marine environments had to rely on trial and error heuristics. The Vik brothers, for instance, meticulously documented their experiments over a six-year period to make sense of various critical dimensions, formulating an idiosyncratic "research program" (Osland, [1990\)](#page-38-7). Apart from generic know-how concerning practical tasks like hatching and nursing, there was little in the way of scientific theory to guide them beyond the fry's initial life cycle.²

In the 1960s there was little evidence that large-scale salmon farming was feasible and could make a significant contribution to rural coastal economies, so at first, there was scant assistance to be had from the

²Salmon mariculture began almost in parallel on both sides of the Atlantic in the late 1950s (Nash, [2010\)](#page-38-2). Attempts with Pacific salmon in the US around the Puget Sound to boost fisheries were plagued by disease and saw little success in comparison.

Norwegian public sector and its knowledge organizations. Marine biologists doubted the salmon's ability to develop roe in saltwater, and the fisheries inspector at the time, Joakim Harstad, was known for his pessimism. Even the Rural Development Fund, the only public funding source supporting these startups, cautioned against investments in this new enterprise (Osland, [1990\)](#page-38-7). Despite an urgent need for more reliable knowledge on the biology, production technology and economics of salmon farming, there were no formal organizations that could disseminate the necessary knowledge.

Faced with skeptical state representatives, early farmers therefore relied on horizontal, decentralized, and informal peer networks to exchange practical knowledge. The Vik brothers, for instance, developed a clever system with three dirt ponds with fresh water, brackish water, and saltwater for gradual acclimatization of their fish. This contraption caught foreign interest, and even attracted the attention of British-Dutch consumer goods giant Unilever, who paid the brothers 20,000 GBP for rights to copy their design and build a similar facility (Møller & Haaland, [2014b:](#page-38-6) 67; Osland, [1990\)](#page-38-7). A condition set by Unilever for this transaction was that the brothers would keep their design a trade secret. However, the duo later admitted that they happily shared their specifications with anyone who showed interest in their work. Further south, in the Bergen area, another group of farmers would entertain weekly meetings in a café to share their latest insight, since they lacked institutions of learning that could help distribute knowledge. It has been suggested that these egalitarian structures for peer-to-peer knowledge transmission were key to explain the success of Norwegian salmon farmers early on, in comparison with countries like Scotland, which quickly privatized research and kept trade secrets strictly within the boundary of firms (although the details here remain disputed, see Berge, [2000;](#page-35-4) Møller & Haaland, [2014b:](#page-38-6) 77).

The Norwegian Fish Farmers Association was established in 1970, as commercial success was on the horizon. Faced with growing popularity, the need for state support, and control, became pressing, and the authorities began to develop services that could provision for these emerging enterprises. But due to the institutional and administrative framework that regulated saltwater and freshwater fisheries in Norway,

central authorities and established scientific institutions came to support the industry relatively late (Chutko, [2011;](#page-36-6) Hovland, [2014;](#page-37-6) Osland, [1990\)](#page-38-7). At the time, the saltwater and freshwater domain were managed by two different institutions, and there was little consensus about which administrative body fish culture should sort under. Should the new enterprise be categorized as a part of the fisheries, or as livestock production? The fisheries were, after all, specialized domains of managerial expertise, and the Norwegian Directorate of Fisheries (*Fiskeridirektoratet*) had grown into an important public agency overseeing the increasingly scientific management of Norway's fishing fleet after WWII.³ One account even suggests that the growth of aquaculture in the 1970s was indirectly financed in part by the over-taxation of fishing stocks in the preceding decade (Berge, [2000:](#page-35-4) 162).

Aquaculture did, in some ways, resemble agriculture and livestock production more than "fish-hunting." Thus, the Department of Freshwater Fisheries (*Fiskeetaten*), sorting under the Ministry of Agriculture, could be a suitable body for oversight, although outputs from fish farms were dwarfed in size by marine fisheries. Established as early as 1855, over three decades before the authority for marine fisheries, the agency for freshwater affairs had been an official research and management institution since 1910, divided into a practical administrative and a scientific branch populated by university-trained biologists. It had also merged with *Statens Forsøksvirksomhet for Ferskvannsfiskeriene*, a public experimental facility for freshwater fish in 1945. The freshwater agency wielded biological expertise on the early lifecycle of anadromous fish, and managed commercial and recreational freshwater fisheries of economic and cultural value. In postwar Norway, watersheds had been targets for expanding hydroelectric power infrastructure, and licenses for these constructions required developers to guarantee the health of riverine fish populations. But despite being competently staffed, *Fiskeetaten* was no clear candidate for managing the growing numbers of fish farms. Agricultural authorities, the freshwater bureau included, had displayed little interest in marine aquaculture at first, and when they got interested,

³This effort was supported Michael Sars, his son Georg Sars, and Johan Hjort, who made substantial contributions to the fields of marine science and fisheries management.

they had few resources to support the farming communities. Furthermore, the pioneering fish farmers sought political independence from the agricultural establishment, which they considered conservative and stagnant.

One consequence of this institutional schism was a delay in a concise scientific research program for salmonid aquaculture in the early days of industrial expansion. Researchers from the Norwegian Agricultural College, for instance, were primarily interested in the breeding properties of fish from a genetic perspective, and failed to collaborate on a joint research station for aquaculture with scientists at the Institute for Marine Research, who were curious about the industrial potential of aquaculture (Møller & Haaland, [2014c\)](#page-38-8). Fortuitously for the farmers, the disagreement led to the establishment of two independent, but highly productive, research stations for aquaculture science.

While a parliamentary interpellation from 1961 proposed that the Institute of Marine Research should take responsibility for the field in the early phase, it was still nearly a decade before scientific institutions got seriously involved. Historian Nils Kolle suggests that biologists first became interested in the topic after fish farmers approached them directly for science-based advice [\(2014c:](#page-37-7) 147). However, it soon became clear that research on aquaculture offered individual scientists, academic departments, and research institutions an opportunity to position themselves in an exciting, future-oriented field, with promising commercial applications. And while the managerial and research infrastructure for aquaculture lagged half a century behind those of agriculture, they grew fast once established in the early 70s, as those in leadership positions saw benefits in constructively engaging with the fish-farming community. Soon, research groups and even entire departments dedicated to salmonid aquaculture were established.

A shift in science policy was also imminent, as the research had to benefit the growing industry. New research stations were needed to run controlled experiments on breeding, disease, physiology, and production technology. Furthermore, national scientific organizations and institutions of higher learning had to address an increasing knowledge gap. A state commission led by Nils Lysø, a former fisheries minister and county governor, was therefore convened in 1972. Their mandate was

to investigate the prospects of aquaculture and suggest policies to help develop these businesses. Surprisingly, this work took five years and was not finished before 1977. In part, this was caused by the commission's failure to keep up with rapid developments in the field, and partly due to tensions between agricultural and fisheries interests that delayed the outcome (Kolle, [2014b\)](#page-37-8). Farming practices were even expanding so profusely that a temporary regulation had to be put in place in 1973, to gain *some* control.

One of the commission's main legacies was the institutionalization of salmon as two different entities under the Norwegian management regime: a *wild* salmon managed by the freshwater authorities (now sorting under the Ministry of Environment's Environmental Directorate), and a *farmed* salmon to be managed by the saltwater authorities, sorting under the Ministry of Fisheries. The Lysø-commission also discussed the need for guidance services, educational institutions, scientific research on fish health, breeding and production technology. In their 1977 report, the commission also formulated an explicit policy objective: to retain local ownership through decentralized, smaller firms, and maintain fish farming as a sideline for people in coastal areas. The reigning political consensus was based on a social contract that saw individual farms mainly as self-sustaining economic units, contributing to rural development. Capital investments were therefore actively discouraged by regulating who could own farms, and the size of ownership. All market exchange was also recommended to proceed via a centralized sales organization. Clearly, Norwegian salmon farming was never intended to be a global industry based on foreign capital investments.

Although some of these recommendations were controversial, the commission deeply influenced the sector's development in the next years, and key principles from their proposal were formalized in the Aquaculture Act of 1981. However, since salmon farming grew faster than the commission predicted, industrial liberalization followed before long. A legal revision in 1985, for example, removed the owner-farmer principle. Then, as production tripled between 1987 and 1990 without a similar increase in market demand, massive overproduction became a reality. This was partly a consequence of a regulatory regime that disincentivized farmers to pace their production according to market demand. The result

was a total collapse of the salmon market in 1990–1991, and a major crisis in the industry. Soon, a national restructuring of the entire salmon industry followed. Through a series of bankruptcies and mergers, farm ownership was suddenly concentrated in significantly fewer companies than before. More deregulations followed in 1991, before the industry again faced a period of re-regulation in 1996, as a new feed-quota system was introduced to prevent overproduction from happening again. This quota system was abolished in 2005 in favor of a new management protocol based on a principle of maximally allowed biomass (*maksimalt tillatt biomasse, MTB*), instead of feed quotas. It is a version of this principle, which determines how much biomass of living fish is allowed in the sea per concession, that regulates the industry today.

Foregrounding Fish Health

Rapid growth of salmon production in the late 80s and early 90s was not a result of Norwegian authorities handing out an abundance of farming concessions. Instead, it was enabled by improvements in production technology. Backed by intense research to optimize the production process, salmon mariculture was launched on the path toward industrial triumph, with a landed value of roughly 64.5 billion NOKs in 2018.

At first, farming pens were makeshift rectangular wooden structures, with seines attached to them. Eventually, these were replaced by more versatile octagonal pens, where the fish could swim in circles, demonstrating formidable growth (Berge, 2000).⁴ Then, in 1974, the production of a polyethylene construction known as the Polar Circle-pen began in Northern Norway. This novel design, which replaced wood, was soon exported to fish farmers abroad. Based on modern materials, these new contraptions were less capital intensive than land-based ponds or fenced-off saltwater inlets, which required elaborate technical arrangements. Plausibly, innovation in pen technology was based on knowledge transfer from the saltwater fisheries (purse-seiners, in particular), which

⁴The design was called "Grøndtvedt-pens," after two pioneering brothers on the island Hitra in Trøndelag County (Osland, [1990\)](#page-38-7).

had accumulated experience about keeping fish in nets and transferring live fish into well boats. New plastic technologies also appeared, and lightweight materials such as polyethylene, PVC, and fiberglass revolutionized the production and design of life-support systems, not just for marine fish culture, but also for wet laboratories and hatcheries (Nash, [2010:](#page-38-2) 170). The growing supply industry became important translators of scientific insights produced by research institutions and universities.

Meanwhile, public research institutes invested heavily in national breeding programs based on the population genetics of salmon stocks. This effort enabled farmers to select brood fish for attractive traits such as growth rate, sexual maturation, meat quality, and other heritable attributes affecting production and quality. Additional biological research uncovered the environmental parameters that made the fish grow healthily, while maintaining high quality and an attractive appearance for consumers. New hand-held measurement devices also became available for analyses that before required entire laboratories to perform.

The logistics of fish feeding, which had become a massive bottleneck, exemplify this progress. Initially, farmers experimented with manually grinding and mixing fish with nutritional additives, sometimes using cement blenders. One widespread approach included freezing the resulting dough in chunks that could be hand-fed to the pens. Later, dryfeed pellets, developed by the agricultural company Skretting in 1963, significantly eased the logistics of feeding. Automatic feeding systems became reality a decade later. This technology also spurred research on nutritionally enriched feed components which reduced the salmon's "feed conversion ratio"; a measurement of how effectively animals convert feed mass into productive output. Lien suggests that this humble feed pellet offered farmers a kind of "time machine," whose transformative powers made salmon farming into a scalable enterprise [\(2015:](#page-37-2) 120). By detaching water from the marine feed resources, decay was halted, which enabled shipments and storage of marine resources across vast distances in concert with new trade agreements and value chains.

The entrepreneurs who switched their production habitat from freshwater to marine cultivation faced less complications with fish diseases than in freshwater, at first. But any illusions about the ocean being a disease-free environment were soon shattered. These first farmers usually lived near the ocean, and often positioned their pens so that they could literally monitor their facilities from their own living rooms. And due to this pragmatic choice, pens tended to cluster together in areas where water circulation was poor, with low flowrates and in close proximity. In itself, fish farming at sea does not create new diseases, but pathogens can move over large distances in the marine environment, and high concentrations of animals in a small area, combined with lax hygiene, can lead to horizontal outbreaks from infectious agents that cause little mischief in the wild. Farming pens use nets to contain fish, and these containers can freely exchange their contents with the surrounding water mass. When the industrial expansion was scaffolded by new technology that increased fish densities per unit of volume, the risks of epizootic transmissions also escalated. In turn, new technologies of governance, area planning, and work on preventive fish health with new vaccines, became crucial to tackle the inevitable disease problems that followed. These developments exerted strong pressures to streamline and standardize production.

Although salmon lice had become a nuisance for farmers, it was other fast-acting and lethal infectious diseases that first caught their immediate attention (Kolle, [2014a\)](#page-37-9). Since other production factors were insignificant if the produce perished from disease before it was sold, fish health quickly became a key determinant for economic success. The Fish Disease Act from 1968 legislated the protection of wild fish against diseases by placing restrictions on imports and provided veterinarians with a monopoly to prescribe medicines. But this regulation was soon inadequate, and some stakeholders worried that impressions about poor hygiene could jeopardize the reputation of farmed fish among consumers. Mortality rates in the freshwater phase of the life cycle, for instance, fluctuated between 10 and 70% as late as in 1987 (ibid.). We saw that the Lysø-commission received support for an intermediary Concession Act in 1973, until a permanent law was worked out. Besides offering a regulatory mechanism in accordance with the commission's political vision, this concession schema also provided a legal basis for fish health and hygiene. This intermediary act was an instrument that

public administrators could wield to regulate and plan new farming facilities, by establishing minimum distances between neighboring facilities to prevent disease transmission, for instance.

Since pathogen dynamics are determined by factors like water current, temperature, farm densities, and other "local" characteristics, salmon production was a context-sensitive operation from the beginning. In 1974, as much as 90% of cultured fish suffered bacterial infections of *Vibrio salmonicida*, manifesting in the form of pale gills and skin lesions. Then, in 1976, the eponymous Hitra-disease erupted on an island outside of Trøndelag county, in Central Norway. Also caused by *V. salmonicida*, later known as "cold-water vibriosis," these outbreaks decimated several farms in 1979. Affecting as many as half of all Norwegian farms, the disease left a trail of bankruptcies.⁵ Antibiotic remedies became the only viable solution to these problems, and its consumption skyrocketed in the late 1980s, as a tremendous growth in production volume brought these biological vulnerabilities into the light. By the end of the decade, fish health emerged as a paramount concern, as bacterial infections like furunculosis, vibriosis, and viral diseases such as infectious salmon anemia and infectious pancreatic necrosis, threatened the industry with extinction (Kolle, [2014a\)](#page-37-9).

Out of this precarious situation, a new cultural consensus soon emerged. To build a viable industry, medicinal treatments had to become the last resort. Prophylaxis, based around the science of fish health, immunology, and vaccination schemes, was institutionalized as a foundational management principle. In 1983, a major initiative to harmonize efforts, called Healthy Fish (*Frisk Fisk*), was launched by an association of farmers in collaboration with the national sales cooperative. Lasting until 1996, several vaccines against the most prevalent diseases were developed under the umbrella of this initiative. In 1990, a new law for coordinating and regulating fish disease management (*Fiskesykdomsloven*) in marine captives was also put in place, expanding on the old law of 1968, which only covered freshwater fish. R&D investments in this phase were also significant, as funding increased from 50 million NOK in 1984 to

⁵A costly two-year battle ensued over the approval of a vaccine against *Vibrio salmonicida* between the University of Tromsø, who developed it, and the Veterinary Institute in Oslo, who was mandated with approving the treatment.

300 million in 1989 (Kolle, [2014a:](#page-37-9) 186). The University of Bergen and the University of Tromsø also created new professional degrees in "fish health biology" ("aquatic medicine," *fiskehelsebiologi*), in dialogue with the industry. A protected title only granted to those with a five-year specialization, the fiskehelsebiolog complemented the work of regular veterinarians, and soon occupied key managerial positions in hatcheries and farms. Established in 1989, it took 18 years and a long professional struggle with veterinary authorities, before these so-called "fish doctors" were given prescription rights for fish medicines.⁶

The transformative effect of this concerted cultural and technological change on fish health should not be underestimated and is illustrated by the following numbers. In 1987, farmers spent almost 50 metric tons of antibiotics on roughly 54,800 tons of total production, less than 5% of today's annual production. In comparison, the use of antibiotics in the period between 2013 and 2017 hovered between 201 and 860 kilograms, on an annual volume of produce averaging over 1.2 million tons.

The threat posed by salmon lice to the welfare of fish reared in captivity, along with its possible negative effects on wild stocks, also came under increased public scrutiny in the 1990s. While obviously afflicting the fish kept in pens, the parasite was also suspected to be a major cause behind an observed decline in wild salmon populations. Smaller fish seemed particularly vulnerable to lice attacks. Now spread in clusters along the coast, salmon farms were suspected to cause an increase in infection pressure on wild salmon, by functioning as host reservoirs. Here, large amounts of parasites could proliferate and potentially exacerbate the mortality of smolts during their migration from the rivers to the ocean.

As part of a cultural shift toward a preventive approach to pest management, a National Action Plan Against Lice (*Nasjonal Handlingsplan mot Lus på Laksefisk*) was launched in 1996, with support from The Research Council of Norway. The plan was designed by a commission of representatives from farming companies, governmental agencies, as well as scientific and other professional organizations. Eventually, this strategy

⁶The Norwegian seafood industry had long pushed for a closer integration with the European Single Market. Paradoxically, prescription rights for fish health biologists were partly delayed due to European Economic Area regulations (Hersoug et al., [2012\)](#page-37-10).

was codified, and a series of regional administrative regulations were introduced. These placed upper limits on the average amount of lice per fish that were allowed in farms, before antiparasitic treatment would have to be initiated. In 2000, these regional regulations were unified under a national law aimed at reducing lice infections (*Forskrift om bekjempelse av lakselus*). When the public food-hygiene regimen was reorganized as the Norwegian Food Safety Authority in 2004, fish health work in general, and the lice issue in particular, was placed high on the agenda with highly detailed and mandatory reporting schemes.

Increased focus on salmon lice as a management problem also coincided with a strong push to revitalize aquaculture science toward the end of the millennium, as funding opportunities for scientific research began to wane. Some stakeholders even worried that a lack of public R&D support could engender a chasm between practitioners in the industry, and the relevant scientific communities (Hersoug, [2014a\)](#page-36-7). This call for more funding was answered and aquaculture was increasingly prioritized in national research policies and strategies around the turn of the millennium. Sophisticated biotechnological research, in particular, such as the mapping of the salmon genome, was considered essential for keeping *Lakse-Norge* economically competitive, and to seize national control over a valuable commodity in the emerging "bioeconomy." Between 1999 and 2003, funding for marine R&D was higher than any other scientific domains, with public funds representing 76% of total R&D investments in the field (Hersoug, [2014b:](#page-36-8) 307). These numbers tripled over the next years, seeing up to 7% annual growth, thereby exceeding the relative growth of the Norwegian GDP, and funding for other scientific fields in the same period.

But although marine aquaculture was prioritized in national research programs, the industry's growth ambitions called for even more problemsolving. Knowledge to accomplish this would be derived through scientific means, but instead of academically focused on epistemic virtues like research publications in prestigious journals, it would primarily be oriented toward practical applications (ibid.: 308). So, although farming companies differed in their levels of commitment to R&D investments, the Norwegian Seafood Federation eventually called for the establishment of a research fund to be financed by a tax of 0.3% on all seafood exports. Organized as a limited company, owned and supervised by the Ministry of Trade, Industry and Fisheries in 2001, the Norwegian Seafood Research Fund would complement public funds, based on valueadding priorities set by a board of representatives from three industry advisory groups.

Managing Salmon Lice: Coevolution and Resistance

Salmon lice were likely among the first major pests that salmon farmers could directly observe on their livestock, after transitioning from freshwater to saltwater culture. At first, they were at a loss about how to cope with the infections, but a solution eventually presented itself in the form of a compound known as trichlorfon, sold under the brand-name *Neguvon*. The organic compound, which belong among the so-called organophosphates, was originally used for antiparasitic treatments of pigs and was dissolvable in water. A citation from a correspondence on treatment regimens for *Neguvon* in the journal *Aquaculture* from 1977, illustrates the urgency: "In sea farms, however, where large numbers of salmonids are kept under confined conditions, the parasite has every possibility for mass infection. Attacks with several hundred parasites per fish have been recorded, and over 2000 parasites have been counted on a single Atlantic salmon" (Brandal & Egidius, [1977:](#page-36-9) 177).

Over the years, a stream of new remedies against the parasite were deployed under veterinary auspices (Aaen et al., [2015\)](#page-35-5). The majority of these worked by disrupting neural signaling or chitin synthesis, crucial for the development of arthropod exoskeletons during molting. *Neguvon* was first administered orally, but farmers later switched to bath treatments due to difficulties with controlling the intake through feeding. Then came natural pyrethrin-baths (*Py-Sal*), using an oily substance as an impractical "top dressing" on the fish pen (Torrissen et al., [2013\)](#page-39-3). Next, dichlorvos was used, an organophosphate first introduced among Scottish farmers as *Nuvan*. Baths of hydrogen peroxide followed, a powerful oxidant that disrupts cell membranes, with narrow safety margins. In the late 1980s, lice infestations intensified, and farmers

turned to ivermectin. The compound showed a prolonged effect but also had low safety margins. Diflubenzuron (*Lepsidon*, *Releeze*) entered the scene in the early 90s, while its relative teflubenzuron (*Ektobann*) appeared a decade later. The drawback of this drug was that the effect was exclusively restricted to the early developmental stages of lice. Another organophosphate, azamethipos (sold as *Salmosan*), was introduced in 1994. Then bath treatments with synthetic pyrethroids such as cypermethrin (*Excis*, *Betamax*) and deltamethrin (*Alpha Max*) followed suit, showing better effects and safety margins than many other drugs.

The compounds deployed against salmon lice all had their pros and cons: some were easy to administer, while others only worked on specific stages of the lifecycle. A few were highly toxic, with low safety margins both for the livestock and for the humans tending them. But common for these therapeutics was the fact that salmon lice would eventually develop reduced sensitivity toward all the drugs after prolonged use. Organophosphates, for example, lost their efficacy already in the mid-90s, while the class known as pyrethroids lasted roughly a half decade longer. Many farmers, weary of the constant struggles against their parasitic interlocutor, hoped they had a silver bullet when a compound named emamectin benzoate appeared in 1999. Sold under the brand SLICE, and belonging to a class of insecticides called avermectins, which are fermentation products from the bacteria Streptomyces avermitilis, the substance disrupts mechanisms involved in transmitting nerve impulses, causing paralysis and death.

At first, SLICE was a godsend for farmers, but between 2002 and 2006, a trend suggesting gradually reduced efficacy was evident, and finally, the parasite forcefully demonstrated resistance against all the chemotherapeutic treatments maintained by farmers in their arsenal. And despite efforts to bring a new chitin-synthesis inhibitor called Imvixa (lufenuron) to market, no new drugs have entered the Norwegian market after SLICE as of yet.

A Mutual Causation Process

The story of salmon lice in modern aquaculture is one of coevolution: "Intensive farming creates conditions for parasite growth and transmission drastically different from what parasites experience in wild host populations and may therefore alter selection on various traits, such as life-history traits and virulence" (Mennerat et al., [2010:](#page-38-9) 59). Drug resistance is an extension of this process, as human interventions exert strong selection pressures on certain genotypes in a naturally abundant parasite population through ever more technology- and knowledge-intensive farming practices.

The evolutionary mechanisms at play here are similar to those propelling the familiar case of antibiotics resistance in human medicine. Individuals in a given salmon lice population vary in their sensitivity to chemicals. When interventions are made with chemotherapeutants to reduce infections in pens, as farmers must abide by current regulations, they never successfully eradicate all the lice in single a location. Often, some specimens survive because they possess mutations that reduces their sensitivity to the administered treatment. Such genetically based resistance mechanisms work by point mutations in the genetic pathway that is targeted by the antiparasitic chemical. This, in turn, results in either protein insensitivity, up-regulation of genes for detoxifying metabolism, biochemical modifications of cellular pumps that reduce uptake of medicinal compounds in feeds, or by modifying the organisms' cuticle thickness, which physically shields the animal against chemicals (Aaen et al., [2015:](#page-35-5) 73). Lice that possess such traits will display increased fitness in an environment where antiparasiticides are frequently used. Their offspring may then inherit genotypes that on average are less drug sensitive than those carried by the ancestral population. As such, multiple rounds of selection may breed a new population of "super-lice" over time, ever more resistant to the treatments they are exposed to.

These dynamics, which severely complicates lice management, are in part driven by cultural practices meant to ensure fish welfare, as regulations change rapidly to keep up with the biological complexities of farming pens. For example, between the summer of 2008 and January 2013, the law was revised five times in four and a half years, ushering

in a new regulation every 10 months. Taking an evolutionary point of view, this sets up a culturally driven feedback mechanism that is likely to reinforce resistance to key therapeutics, as fish farmers have no other recourse than to deal with the short-term logic dictated by various legal instruments that requires them to maintain lice numbers under a fixed threshold.

The fight against drug-resistant lice thereby becomes a race against millions of mutagenic events that occur every time the population of salmon lice reproduces. Adding to the challenge, the many hundred fish farmers along the Norwegian coast also rely on a collection of idiosyncratic practices used to conform with lice regulations and pest management, which makes coordination of pesticide use challenging. As one fish health biologist explained, it is not uncommon that farmers develop local drug regimens that deviate from the guidelines of the drug manufacturers and those who prescribe the medicine. Doubtlessly, the aqueous environment adds a layer of complexity to pest management (Nash, [2010\)](#page-38-2). As farming takes place in open nets along the coast, lice strains can, in some conditions, quickly spread from one area to other sites. Therapeutic actions taken by a farmer in one area may therefore have cascading effects on the population dynamics of lice in neighboring farms. Resistance against emamectin benzoate, for instance, likely originated from a single progenitor, and then swept across the entire Atlantic lice population in a period between 1999 and 2010 (Besnier et al., [2014\)](#page-36-10).

The idea of "coevolution" offers a conceptual frame to articulate inseparable relations between the cultural transmission of knowledge among human actors, and the expansion of drug resistance in lice. In its traditional formulation, coevolution is defined as "the evolution of complementary adaptations in two species caused by the selection pres-sures that each exerts on the other" (Martin & Hine, [2015\)](#page-37-11). More recently, anthropologists have stressed the importance of cultural practices in transforming environments where biological selection takes place, introducing the notion of "gene-culture co-evolution" or "dual inheritance theory." This framework suggests that cultural transmission of socially learned information plays an active part in driving natural selection, a familiar example from our history of animal domestication being a culturally induced selection for lactose tolerance ("lactase persistence")

in groups that took up herding and milking (see Henrich, [2015](#page-36-11) for a catalogue of examples). Drug-resistant salmon lice presents a variation on this theme of culturally induced coevolution, with drug resistance occurring in a parasite that torments another species under our care. In this case, the lice population responded to novel human interventions in the farming pen with an alternate biological constitution. The human response, on the other hand, was delivered through a shift in institutional reality, that introduced novel interventions that were often derived from the best available scientific knowledge.

These enduring interactions between people, lice, and salmon give rise to what Merrill Singer describes as a "mutual causation process" [\(2014:](#page-39-7) 1280). This is a situation where species A engages in some novel behavior, like human farmers attempting to domesticate salmon. In turn, this facilitates responsive changes in species B, as vast amounts of salmon are concentrated in densely populated pens. This affords species C with new opportunities, such as rapid proliferation due to an unprecedented abundance of salmon hosts. New actions are then elicited from species A, like the intensive use of parasiticides. Consequentially, species C responds by evolving genetic adaptations making certain individuals highly resistant to the compounds. In retaliation, species A then takes new epistemic and pragmatic actions, entering a mutual causation process that may extend ad infinitum.

Just as many fish diseases mutate in ways that require modifications in the design of vaccines to overcome new biological adaptations, salmon lice management provides fish health experts with an "eternal market" due to its remarkable ability to adapt to antiparasitic interventions. In this case, cultural responses to the lice problem, such as political decision-making, laws and animal ethics occasionally informed by scientific knowledge, become driving factors for the biological selection of resistant salmon lice, because they impel farmers to take mitigating actions that propel the mutual causation process forward. The precarious nature of this dynamic was described in frank terms by an entrepreneur from a major fish health consultancy in an article from a Norwegian business daily, aptly named "Loaded on a lousy salary": "I make money out of every new lice-legislation the authorities enforce, but I don't know why we should make money on this. More control does not result in less

lice and does not help wild salmon. The only people making money from this are those who are selling lice-therapeutics. Salmon lice has created a whole industry" (Ytreberg, [2015\)](#page-39-8).

The entrepreneur's ambivalence stems from the fact that Norwegian salmon farmers have been subjected to a host of new regulatory regimes since the turn of the millennium that have significantly reduced local decision-making power. This includes a comprehensive audit culture. One study found that a fairly typical farming company filled out approximately 1300 official forms in a single year (Normann et al., [2005:](#page-38-10) 1). Under the current legal regimen, farmers are obliged to conduct weekly assessments of lice levels, and therapeutic interventions are prescribed where lice counts exceed an average threshold of 0.5 adult female lice per fish. National monitoring and reporting schemes, administrated by the Norwegian Food Safety Authority, also work to ensure that farmers along the coastline comply with these management systems, and every [week the latest data is made publicly available online \(see:](http://lusedata.no) http://luseda ta.no).

Given that technical progress has enabled massive increases in production volume by shortening the period from fish egg to finished product, despite current caps on maximally allowed biomass, one could argue that the present concession system offers a rather weak management mechanism. However, in the absence of efficient therapeutics against lice, Norwegian authorities will not allow salmon farmers to expand production beyond current numbers, despite political imaginaries projecting a fivefold increase in the future to capitalize on the soaring global demand for fresh fish.

In response to this grave situation, new interventions by farmers, based on an abundance of scientific research, aim to augment management practices in ways that minimize or circumvent the problem of therapeutic resistance. Consequentially, there are scores of inventive solutions in progress, ranging from anti-lice-attachment feeds to cleaner fish, as well as novel chemotherapeutic regimens and various mechanical delousing systems. For instance, significant investments have been made into closed containment systems for use at sea, while some have proposed to move the entire production process onto land in special plants. On the more technology-intensive side, one company has even developed

an "optical delousing technique" based on an apparatus that combines machine vision and a laser beam to identify and directly incapacitate louse individuals on salmonids swimming in the pen.

Others have proposed a solution where genomic selection is used to identify more lice-resistant brood fish for cutting-edge breeding programs. Some biologists, however, advise caution due to the differential rates of reproduction between the two species (Jensen, [2010\)](#page-37-12). According to this line of reasoning, farmed salmon has a generation time that lasts roughly three to four years, while that of lice is between seven and ten generations per year. This means that the parasite has a generation time up to forty times faster than its host, so that for every five salmon generation there could possibly be hundreds of lice generations subjected to strong selection pressures. Introducing a new breed of liceresistant fish to the pen can therefore drive the lice population toward a new class of "super-lice," impervious to the salmon's immunological defenses. If this occurs, it is unknown whether farmers can rely on artificial breeding to keep up with the evolutionary arms race. And while this may not constitute a major hazard for farmed salmon, since their lifecycle and reproduction are controlled in captivity, the resulting "super-lice" could jeopardize wild salmon stocks. As with antiparasitic compounds, and other delousing methods where resistance is a probable outcome, breeding is likely no silver bullet.

As summarized by the frank entrepreneur we encountered earlier: "Fantasy has no limits. There's hardly a week without someone calling me about some snake oil-thing against salmon lice. God knows we've tested a lot of weird stuff against lice. We've tested, tested and tested. We flush, we clean, we use lasers, we use skirts and I don't know what the fuck we don't do" (Ytreberg, [2015\)](#page-39-8). This constant struggle against parasitic encroachment in salmon farming demonstrates the open-ended nature of domestication processes (Lien, [2015\)](#page-37-2). Relationships of this kind are even more peculiar given that in nature, even parasites are beset by other parasitic organisms. Salmon lice themselves have been proven to carry an assortment of bacteria, fungal agents known as microsporidia (Nylund et al., [2010\)](#page-38-11), and viruses (Økland et al., [2014\)](#page-38-12). These hyperparasites make their living by parasitizing other parasites. Ironically, some scientists have even proposed that such viruses could, given the right

biotechnological advances, even become potential sources for lice control in the distant future (Nordland, [2015\)](#page-38-13).

Given the convoluted nature of these relationships, human mastery and control seem at best to be ideals that domesticators strive toward, rather than a fixed property of human relationships with livestock. Such precarious exchanges are likely to forever characterize those sites of enactment that Lien describes as a *domus*: "fragile assemblages of beings and things that, as long as they hold together, constitute the conditions of growth and reproduction of humans as well as of nonhuman beings" [\(2015:](#page-37-2) 5). The trajectory of salmon farming from an extensive to an intensive mode of production also highlights how humans and our companion species will continue to face new crises, made more acute by the very success of our own projects. Here, I have offered a "naturalistic contextualization" of the feedback and feed-forward mechanisms acting on biological and social systems in this perpetuating mutual causation process (Singer, [2014:](#page-39-7) 1281).

Antagonistic relationships with parasites have evolved in trajectory with human societies and will likely take part in any future domestication adventures that our species embark on. Such relationships also call for new epistemic projects on a grand scale. Fredrik Barth suggested that the key concern of an anthropology of knowledge should be to analyze the contents of aggregate traditions of ideas, their expression, patterns of distribution and how they come to life through creativity, transmission, and exchange [\(1990:](#page-35-6) 1). With respect to the epistemic work that accompanies a phenomenon like drug-resistant salmon lice, we must also attend to the effects of knowledge, and how content, distribution patterns, creativity, transmission, and change extend back into the biological realm. In this case, scientific insights have acted both as a driver of interventions in the farming pen that cause unintended biological complications, but also offers its means of detection, and a source of future solutions. These feedback loops between the actions of socially positioned agents and evolving biological phenomena are shaped by the representations of knowledge that human agents construct (Barth, [2002:](#page-35-7) 10).

Applications of parasitological knowledge to animals, and eventually marine domesticates, began as offshoots from medical specialties like infectious disease and human parasitology. This field emerged through descriptions of specific infections, identification of disease-causing parasites, accounts of species' lifecycles, and ascriptions of causal links between disease outbreaks and vector transmission. For a long time, the science of parasitology was a subfield of tropical medicine, which sought to understand and control the effects of pathogens in European colonies, and where possible, eradicate their transmission routes through public health work and other interventions. But as part of a general trend where more domains of biological science are increasingly "molecularized," so have parasitology "gone molecular" through the application of cuttingedge genomics research. The science of salmon lice is no exception. Like the parasite's host, the lice genome has been thoroughly mapped (see Treimo, [2007\)](#page-39-9).

The fall of 2016 saw widespread media coverage of heavy lice infestations on a salmon farm located on the northwestern coast of Norway. Reports also suggested that the owners of the farm had failed to take appropriate measures, despite facing a very critical situation. In the media, images of fish with severe skin lesions circulated widely, and commentators decried the event as deeply troubling from an animal welfare perspective. Interviewed about the case in November 2016, Professor Frank Nilsen, one of the world's foremost experts on the parasite, explained that he had not seen lice-related injuries of this magnitude since the end of the 1980s. Finding more effective measures against lice was urgent. In what follows, I situate the reader in the laboratories of the Sea Lice Research Centre, where a group of molecular parasitologists under Nilsen's directorship strive to respond to these urgencies.

Environmental historian Stephen Bocking shows how ecological studies of salmon lice in the Broughton archipelago on Canada's Pacific coast, generated considerable political frictions over the future of salmon farming [\(2012\)](#page-36-12). But in contrast to situated ecological science of this kind, the experimental laboratory of the SLRC operates according to a different, more universalizing logic, which Robert Kohler has described as "placelessness" [\(2002:](#page-37-13) 9). This concept stresses the laboratory's ascribed status as a neutral site, an epistemic virtue, which effectively guarantees the robust credibility of scientific outcomes. When tracing the production of novel scientific meanings in the laboratory,

instead of the salmon pen, we are offered with a quite different perspective on the *domus* of salmon aquaculture, or how humans and farmed animals learn to live well together (Lien, [2015:](#page-37-2) 165). Here, I offer a cognitive ethnography of fundamental epistemic activities involved in this kind of experimental knowledge production. Vigilant about potential industrial applications of their scientific insights, this research community uses state-of-the-art methods to probe the salmon louse and its genome sequence for molecular mechanisms and pathways of target genes that can be mobilized for novel interventions. The hope is to circumvent the pitfalls of past failures to sustainably manage parasitic adaptation in domesticated salmon. Solving these problems of lice management requires further acts of domestication in the laboratory.

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