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Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions

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Abstract

Atlantic salmon (*Salmo salar*) is one of the best researched fishes, and its aquaculture plays a global role in the blue revolution. However, since the 1970s, tens of millions of farmed salmon have escaped into the wild. We review current knowledge of genetic interactions and identify the unanswered questions. Native salmon populations are typically genetically distinct from each other and potentially locally adapted. Farmed salmon represent a limited number of wild source populations that have been exposed to ≥12 generations of domestication. Consequently, farmed and wild salmon differ in many traits including molecular-genetic polymorphisms, growth, morphology, life history, behaviour, physiology and gene transcription. Field experiments have demonstrated that the offspring of farmed salmon display lower lifetime fitness in the wild than wild salmon and that following introgression, there is a reduced production of genetically wild salmon and, potentially, of total salmon production. It is a formidable task to estimate introgression of farmed salmon in wild populations where they are not exotic. New methods have revealed introgression in half of ~150 Norwegian populations, with point estimates as high as 47%, and an unweighted average of 6.4% across 109 populations. Outside Norway, introgression remains unquantified, and in all regions, biological changes and the mechanisms driving population-specific impacts remain poorly documented. Nevertheless, existing knowledge shows that the long-term consequences of introgression is expected to lead to changes in life-history traits, reduced population productivity and decreased resilience to future challenges. Only a major reduction in the number of escapees and/or sterility of farmed salmon can eliminate further impacts.

KEYWORDS
aquaculture, evolution, fish farming, fitness, genetic, hybrid

1 | INTRODUCTION

Natural resources are increasingly exposed to anthropogenic pressures that compromise or threaten their persistence. The Millennium Ecosystem Assessment (Anon 2005) identified five major threats to native plants and animals: habitat change, climate change, invasive species, over-exploitation and pollution. Not included on this list, but an increasing problem, is the interaction between wild populations

and their domesticated conspecifics (Hindar, Ryman, & Utter, 1991; Hutchings & Fraser, 2008; Laikre, Schwartz, Waples, Ryman, & Ge, 2010; Randi, 2008). While not fitting exactly into one of the Millennium Assessment categories, it is related to the type of challenges posed by invasive species and problems that stem from over-exploiting wild populations. Furthermore, many of these stressors can interact with each other to exacerbate the negative impact of a single cause, for example the combined impact of the release of captive-bred fish and climate change on recipient wild populations (McGinnity et al., 2009).

As exploitation of wild living resources becomes increasingly unsustainable (Hutchings, 2000; Myers & Worm, 2003), domestication and captive production of the same species intuitively represents an obvious alternative (Teletchea & Fontaine, 2014). However, when selective breeding programmes are undertaken, and releases or escapes occur into the wild, there is potential for direct negative genetic impacts on wild populations from gene flow. This problem has been acknowledged for a long time in a variety of organisms (Ellstrand, Prentice, & Hancock, 1999; Randi, 2008), but has been found to be particularly serious in fishes, where harvesting wild populations is replaced by large-scale aquaculture production, as in salmonids. Salmonids represent a continuum of both the quantity and technological concerns associated with their production (Lorenzen, Beveridge, & Mangel, 2012).

At one end of the scale, wild populations may be deliberately supplemented by stocking hatchery-reared offspring of local or exogenous origin that have only been briefly exposed to the cultured environment; this procedure is particularly applied in North America, where hatcheries located on individual rivers are used for propagating offspring of returning spawners (Kostow, 2009). At the other end of the scale, wild populations may be accidently exposed to escapees from farming operations where the fish are non-local, and have been subject to all aspects of domestication, including directional selection for economically important traits. As selection programmes increasingly cause genetic divergence between captive and wild populations for biologically important traits, then the potential for negative genetic consequences of interbreeding between wild and farmed fish also increases until their fitness in the wild becomes severely compromised (Baskett, Burgess, & Waples, 2013; Huisman & Tufto, 2012). In Atlantic salmon (*Salmo salar*, Salmonidae) (hereon referred to as salmon), these issues have been so pervasive that it has emerged as a major model for studying genetic interactions between farmed and wild organisms.

The commercial production of salmon for human consumption first started in the late 1960s in Norway when smolts were placed into sea cages by the company Mowi A/S in Bergen in 1969 and by the Grøntvedt brothers on Hitra in 1970 (Gjedrem, 2010; Gjedrem, Gjoen, & Gjerde, 1991). Since the pioneering days in the early 1970s, rapid and almost continual growth has meant that this industry has now achieved status as one of the world's most economically important industries within the fisheries and aquaculture sectors (Bostock et al., 2010). In 2014, global production of salmon exceeded 2.3 million tons with Norway (1.26 million tons), Chile (0.62 million tons) and the UK (0.165 million tons) representing the primary producers (FAO 2016) (Figure 1). In total, 10 countries produced more than 10,000 tons in 2014.

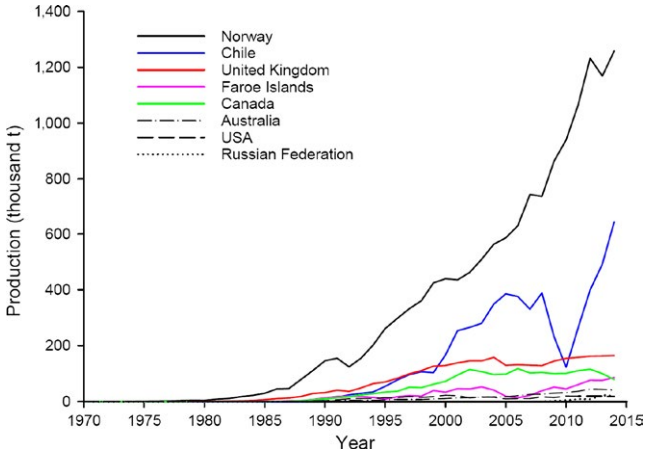

FIGURE 1 Aquaculture production of Atlantic salmon based on the eight largest global producers in 2015

Globally, the production of farmed salmon was rated as number eight by amount for aquaculture fish species, and was by far, the most valuable cultured fish species in 2014 (14.6 billion USD (FAO 2016)). Today, more than 99% of all salmon consumption arises from aquaculture production, and the reported wild catch is as low as 1/1000 of the reported aquaculture production (FAO 2016). As a form of food production, aquaculture is being increasingly considered as one solution to the world's growing demand for protein (FAO 2016), although not all share this optimism (Bovenkerk & Meijboom, 2012; Merino et al., 2012). Nevertheless, commercial aquaculture, including salmon farming, continues to expand globally.

The phenomenal expansion of the salmon aquaculture industry has not occurred without meeting a diverse array of sustainability-related challenges along the way. Farmed escapees may result in both ecological (Jonsson & Jonsson, 2006; Thorstad et al., 2008) and genetic interactions with wild populations (Ferguson et al., 2007; Hindar et al., 1991). In addition, impacts may extend beyond problems with direct biological impacts, including socio-economic (Liu, Olaussen, & Skonhoft, 2011) and general ethical issues (Olesen, Myhr, & Rosendal, 2011), use of marine resources such as fish oil and fish meal for production of high protein feeds (Naylor et al., 2000; Torrissen et al., 2011), general effects on local ecosystems (Buschmann et al., 2006), benthic community impacts (Kutti, Ervik, & Hoisaeter, 2008), use of chemical agents such as antibiotics and antiparasitical agents (Burridge, Weis, Cabello, Pizarro, & Bostick, 2008) and transfer of parasites to native populations (Krkosek, Lewis, & Volpe, 2005; Torrissen et al., 2013).

Many of these factors, individually or collectively, have potentially important consequences for the persistence of wild salmonid populations. In a meta-analysis of available data, a reduction in marine survival of a range of salmonid species in regions of intense salmon farming activity was observed throughout the Pacific and Atlantic basins (Ford & Myers, 2008). Although the range of challenges linked with salmon aquaculture are diverse, an annual risk assessment of Norwegian salmon aquaculture identified inadvertent accumulation of sea lice from fish farms and genetic interactions with farmed escapees

as the two primary challenges to the sustainable development of the salmon aquaculture industry in Norway (Taranger et al., 2015).

Salmon farming typically involves hatching eggs and rearing juveniles in land-based incubators and tanks during the freshwater stage of the life cycle, then transferring smolts to sea cages in sheltered coastal areas where they are reared until market size and thereafter slaughtered. The production cycle takes 2.5–3 years. While significant advances in robustness of production systems have taken place, technical and operational failures nevertheless occur and are the primary reason for incidences of escapes (reviewed by Jensen, Dempster, Thorstad, Uglem, & Fredheim, 2010). Each year, hundreds of thousands of farmed salmon escape into the wild. Some of these escapees find their way onto the spawning grounds of native populations (Carr & Whoriskey, 2006; Fiske, Lund, & Hansen, 2006; Walker, Beveridge, Crozier, Maoileidigh, & Milner, 2006) and partake in spawning (Carr, Anderson, Whoriskey, & Dilworth, 1997; Lura & Saegrov, 1991; Webb et al., 1993), with the possibility of gene flow from farmed to wild populations.

The fact that large numbers of farmed escapees have been observed on the spawning grounds of some native populations has generated widespread concerns regarding the consequences this may have for the short-term fitness and long-term evolutionary capacity of recipient populations. Several earlier review and synthesis articles have broadly addressed this topic (Ferguson et al., 2007; Heggberget, Johnsen et al., 1993; Hindar et al., 1991; Naylor et al., 2005; Thorstad et al., 2008). Scientific reviews have also been conducted on overlapping topics such as the potential for salmon populations to display adaptations to their natal rivers in a process known as local adaptation (Fraser, Weir, Bernatchez, Hansen, & Taylor, 2011; Garcia de Leaniz et al., 2007; Taylor, 1991), and the potential responses of populations to fisheries and farming induced evolution (Hutchings & Fraser, 2008). In addition, the fitness of hatchery fish produced for deliberate introduction into the wild via supportive breeding has been reviewed (Araki & Schmid, 2010; Araki, Berejikian, Ford, & Blouin, 2008).

There are key differences in the potential for genetic interaction and likely consequences for wild populations, between when the latter are supplemented by deliberate supportive breeding programmes using native broodstock collected from the wild, or when exposed to accidental releases into the wild of non-local, domesticated farmed escapees. The last decade has seen both a rise in concern regarding the direct genetic impacts of farmed escapees and a large number of new studies bearing on this issue, and there is an urgent need to review current understanding. This is amplified by the development of aquaculture production of other species, which also involves potential genetic interactions with wild conspecifics (Glover, Dahle, & Jorstad, 2011; Somarakis, Pavlidis, Saapoglou, Tsigenopoulos, & Dempster, 2013; Varne et al., 2015).

The salmon is viewed as the model system for understanding direct genetic interactions between domesticated and wild fish stocks (Bekkevold, Hansen, & Nielsen, 2006). Given the many years since salmon farming was initiated, it is pertinent to ask several questions regarding the introgression of farmed salmon into native populations. In particular, what do we know, what we do not know, and what should we know? Here, we provide a comprehensive review of the literature dedicated to this topic and discuss the extent and patterns of introgression, in addition to the short- and long-term evolutionary consequences in recipient populations. We concentrate on direct (i.e. interbreeding) as opposed to indirect genetic effects. Finally, we highlight what the major breakthroughs have been in this field of research in the past decade, and what unanswered questions remain.

2 | ECOLOGY PRECEDING INTROGRESSION

2.1 | How many escapees are there in the wild?

So long as facilities are not fully contained, the escape of farmed fish into the wild is inevitable (Bentsen & Thodesen, 2005; Jensen et al., 2010). While the number of escapees has declined over time as a proportion of the number of salmon in farms, it has remained high as production has expanded (Figures 1 and 2). Salmon production is typically based on the following stages: eggs and fry (~3–4 months); juveniles (~6–12 months); post-smolt/adults (~18–24 months) (Wall, 2011). Each of these stages represents different risks of escape that can be expected to vary from farm to farm and region to region.

Most egg and early-juvenile production is conducted in land-based hatcheries. While escapes at this stage have been typically few, the technological shift towards recirculating systems means that only a very low number of salmon escape into the wild at this stage. Thereafter, several approaches have and continue to be used for juvenile and smolt production. Often, fry are reared to the smolt stage in tanks using flow through systems. Escapes of juveniles from such systems may occur. More recently, there has been an increase in the use of tank recirculating systems, which practically eliminates juvenile escapes into the wild. Alternatively, once large enough, juveniles are transferred to open freshwater pens similar to those used to rear post-smolts in salt water but with finer mesh sizes. This approach, rarely used in Norway and Canada, was used extensively in Chile but is now being phased out in support of disease control (Alvial et al., 2012). In contrast, in Scotland, 42 freshwater pen rearing sites underpin the annual production of smolts to the order of half of all fish produced (~20 million) (Franklin, Verspoor, & Slaski, 2012). These cages, like the ones used for on-growing of post-smolts to adults in the sea, offer the greatest opportunities for escape as there is only a net barrier between the fish and the wild.

Escapes of salmon have been documented during the freshwater stage as juveniles, both from hatcheries (Carr & Whoriskey, 2006; Clifford, McGinnity, & Ferguson, 1998a; Stokesbury & Lacroix, 1997) and from freshwater cages (Coulson, 2013; Franklin et al., 2012; Verspoor, Knox, & Marshall, 2016). These escapees may compete directly with wild juveniles for resources (Jonsson & Jonsson, 2006; Thorstad et al., 2008). A portion of the juvenile males that survive can mature precociously and may potentially spawn with wild fish. Juvenile escapees of both sexes that survive may also migrate to sea and return as adults (Lacroix & Stokesbury, 2004) and attempt to spawn with wild fish as mature adults. Detection of returning freshwater escapes, at

least on the basis of superficial morphological characteristics (Lund & Hansen, 1991), is expected to be difficult as they are unlikely to have some of the more obvious diagnostic features of older farmed fish, such as eroded fins or clumped body shape. Escapes of post-smolts and adults from marine cages occur extensively (Crozier, 1993; Glover, 2010) and typically dominate escapees in the wild (although this is region dependent). However, escapees from marine cages first need to migrate back to freshwater before they can potentially spawn and interbreed with native populations.

Official statistics for the reported numbers of escapees are publicly available in some of the regions where salmon farming is practiced, for example Norway and Scotland (Figure 2). These statistics are based on reports by the farmers themselves and, for several reasons discussed below, are likely to underestimate, significantly in some circumstances, the actual number of fish escaping from farms. In support of this claim, DNA methods to identify escapees back to the farm of origin have been successfully implemented in multiple cases of unreported escapes in Norway (Glover, 2010; Glover, Skilbrei, & Skaala, 2008). Similarly, in Scotland, freshwater escapes identified through vaccination marks were not part of a reported escape event (Franklin et al., 2012). Additionally, there is a lack of correlation between the incidence of farmed escapees in Norwegian rivers and the reported numbers of escapees, while in contrast, there is a correlation between the standing stock of fish in farms and incidence of farmed salmon escapees in Norwegian rivers (Fiske et al., 2006). Finally, a recent meta-analysis of catch statistics and tagging studies has estimated that the real numbers of escapees in Norway were 2–4 times higher than the numbers reported by the farmers alone in the period 2005–2011 (Skilbrei, Heino, & Svåsand, 2015). In other countries, the level of underestimation in escape statistics is unknown.

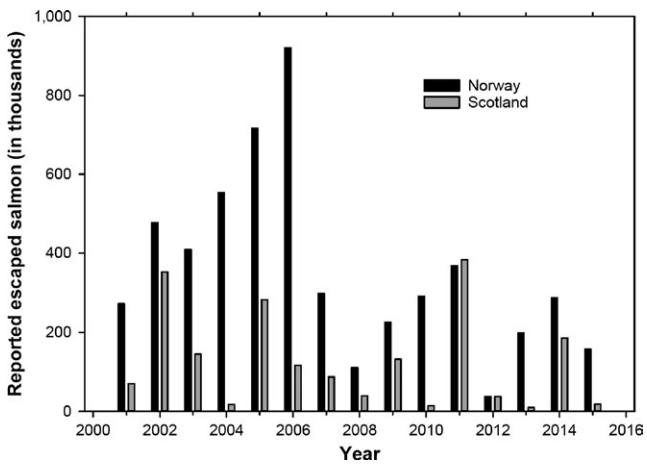

FIGURE 2 Reported numbers of farmed escaped Atlantic salmon in Scotland www.aquaculture.scotland.gov.uk and Norway www.fiskeridir.no in the period 2001 to 2015. Triploid salmon constituted ~54 000 of the 157 000 reported escaped salmon in Norway in 2015, although such statistics are not available for other years. A recent analysis estimated that the correct number of farmed salmon escaping from Norwegian farms in the period 2005–2011 was 2–4 times higher than the official statistics (Skilbrei, Heino et al., 2015)

An analysis of available data from Norway indicates that less than 20% of escape incidents account for more than 90% of the number of reported escapees (Jensen et al., 2010). Despite the fact that large escape events account for a large number of escapees, drip leakage (i.e. multiple small-scale losses usually associated with routine daily activities on farms) may be more important than indicated by the official escapes statistics, considering the under-reporting of farmed salmon escaping as smolts (Skilbrei, Heino et al., 2015).

Each year, hundreds of thousands of escapees are reported from salmon farms across its production range (Figure 2). Given that these statistics are underestimates, it can be reasonably assumed that millions of farmed salmon escape into the wild yearly. In Norway, which produces approximately 50% of all farmed salmon globally, the estimated number of salmon escaping annually from commercial fish farms has probably been in the millions in the period 2005–2011 (Skilbrei, Heino et al., 2015). Put into perspective, the estimated number of wild adult salmon returning to the Norwegian coastline to spawn (i.e. pre-fishery abundance) each year in the period 1983–2014 declined from ~1 million in the mid-1980s to ~0.5 million during the last few years (Anon 2015b). Therefore, in Norway, the only area where data allow such an assessment, the number of salmon escaping from farms is probably in excess of the number wild adult salmon returning to rivers in most years.

The potential for farmed salmon to display genetic interaction with wild salmon will depend on their behaviour after escape. The movements of farmed salmon escapees have been extensively studied in the marine environment (Hansen, 2006; Jensen et al., 2013; Skilbrei & Wennevik, 2006; Skilbrei, Holst, Asplin, & Holm, 2009; Skilbrei, Holst, Asplin, & Mortensen, 2010; Solem et al., 2013; Whoriskey, Brooking, Doucette, Tinker, & Carr, 2006; Zhang et al., 2013) as well as in freshwater (Butler, Cunningham, & Starr, 2005; Carr, Lacroix, Anderson, & Dilworth, 1997; Heggberget, Okland, & Ugedal, 1993; Moe et al., 2016; Okland, Heggberget, & Jonsson, 1995; Thorstad, Heggberget, & Okland, 1998; Webb, Hay, Cunningham, & Youngson, 1991). Available evidence suggests that most escapees from marine cages disappear in the sea and do not return to freshwater (Hansen, 2006; Skilbrei, 2010; Whoriskey et al., 2006). Observation of the empty stomachs in farmed escapees captured in coastal areas (Abrantes, Lyle, Nichols, & Semmens, 2011; Hislop & Webb, 1992), in combination with the lack of change in fatty acid profile in escapees over time (Olsen & Skilbrei, 2010), suggests that escapees from marine cages often struggle to adapt to feeding on natural food items once they are in the sea. In some regions, seal predation is also suspected to cause mortality of the escapees (Whoriskey et al., 2006). While the evidence indicates that survival to sexual maturity of feral escapes is very low, and only a small proportion of escapees manage to survive and enter rivers, the number is often numerically high due simply to the high number of escapees. The actual numbers, however, can be expected to be dependent on both the stage of the life cycle and the time of the year at which they escape (reviewed by Skilbrei, Heino et al., 2015).

An overview of the methods used to identify farmed escapees is given in Thorstad et al. (2008). In short, escapees are typically identified based on external morphological divergence from wild salmon

(e.g. body condition and fin erosion). In Norway, identification of farmed escapees is generally validated by reading scales (Fiske et al., 2006; Lund & Hansen, 1991) and in some cases intra-abdominal adhesions caused by vaccination marks (Lund, Midtlyng, & Hansen, 1997). The relative frequency of adult farmed salmon entering rivers that have escaped into the sea early as opposed to later in the life cycle is variable. Reading fish scales provides an opportunity to identify the stage at which the salmon escaped from a farm (Thorstad et al., 2008). Also, recent developments in fatty acid profiling now make it possible to identify early (those salmon having been in the wild for some time, a year or more before entry to freshwater) as opposed to late (those having recently escaped, and certainly the same year in which they entered the river) escapees accurately (Skilbrei, Normann, Meier, & Olsen, 2015). This method is based on the fact that farmed salmon are fed a diet including a high concentration of terrestrial lipids that are high in medium chain polyunsaturated fatty acids (PUFAs) such as 18:2n-6 (Olsen, Taranger, Svasand, & Skilbrei, 2013) and that its concentration decreases with time after escape (Skilbrei, Normann et al., 2015). Studies using this and other approaches have shown that one half or more of escapees entering freshwater have escaped from farms in the same year that they entered freshwater (Madhun et al., 2015; Quintela et al., 2016; Skilbrei, Normann et al., 2015).

Farmed escapees have been documented in rivers in most regions where there is commercial aquaculture; Norway (Fiske et al., 2006; Fiske, Lund, Østborg, & Fløystad, 2001; Gausen & Moen, 1991; Lund, Okland, & Hansen, 1991; Okland et al., 1995), the Finnish region of the River Teno (Tana in Norwegian) that flows out in Norway (Erkinaro et al., 2010), the UK including Northern Ireland (Butler et al., 2005; Crozier, 1998; Milner & Evans, 2003; Walker et al., 2006; Webb et al., 1991), Ireland (Clifford, McGinnity, & Ferguson, 1998b), Atlantic North America (Carr, Anderson et al., 1997; Lacroix & Stokesbury, 2004; Morris et al., 2008; O'Reilly, Carr, Whoriskey, & Verspoor, 2006; Stokesbury & Lacroix, 1997; Stokesbury, Lacroix, Price, Knox, & Dadswell, 2001; Utter & Epifanio, 2002), Pacific North America (Fisher, Volpe, & Fisher, 2014; Volpe, Taylor, Rimmer, & Glickman, 2000), Chile (Sepulveda, Arismendi, Soto, Jara, & Farias, 2013) and Australia (Abrantes et al., 2011). In addition, escapees have been reported in oceanic feeding areas (Hansen & Jacobsen, 2003; Hansen, Reddin, & Lund, 1997; Jensen et al., 2013), as well as in rivers far away from major farming regions (Gudjonsson, 1991; Piccolo & Orlikowska, 2012). Therefore, escapees display considerable potential for long-distance dispersal/migration. That said, in Norway, the incidence of farmed escaped salmon in rivers is correlated with the volume of farming within that region (Fiske et al., 2006), and, in Scotland, lower numbers of escapees occur in rivers on the east coast, where there are no marine salmon farms, than on the west coast where farming occurs (Green et al., 2012; Youngson, Webb, MacLean, & Whyte, 1997). Specifically for juvenile escapes, there is a close link between their presence in rivers and nearby hatcheries (Carr & Whoriskey, 2006; Clifford et al., 1998a) or freshwater cages (Verspoor et al., 2016).

A Norwegian study based on reading fish scales from summer angling surveys, as well as dedicated autumn angling surveys, in the period 1989–2004 reported weighted mean annual per cent of farmed salmon in a cross section of rivers between approximately 0%–6% and 2%–30% for the two survey types, respectively (unweighted averages were 2%–12% summer, 9%–32% autumn) (Fiske et al., 2006). A new monitoring programme for escapees was established in Norway in 2014, and based on data from several survey methods (summer angling, autumn angling, autumn snorkelling), 30 of the 140 rivers surveyed in 2014, and 17 of 165 rivers surveyed in 2015 displayed an observed frequency of >10% escapees (Anon 2015a, 2016). This gave unweighted averages for summer angling surveys of 5.4% and 3.4% and dedicated autumn angling surveys of 11.2% and 9.1%, in 2014 and 2015, respectively. These numbers are similar to those reported for straying rates of wild and hatchery-produced salmon (Stabell, 1984).

In regions outside Norway, such as the UK and Ireland, catch statistics have also revealed significant numbers of farmed escapees in the rivers (Walker et al., 2006), but in many cases, less than the numbers typically observed in Norway. For example, an analysis of all available data for rivers in Scotland in the period 1991–2004 (or as sampling data allowed), illustrated that the per cent of farmed salmon were typically less than 1% for many rivers and years, although exceptions as high as 10% were observed. Whether these differences to the frequencies observed in Norway are meaningful, however, is uncertain, as methods used for the enumeration of farmed fish in Scottish rivers is often based on morphology without validation using scale analysis. In Northern Ireland, large numbers of escapees have been observed in single rivers in years following single large-scale escape events (Crozier, 1993), and this is also the case in other countries where single events have resulted in large number of escapees in some rivers in some years. In many rivers in Atlantic North America, the numbers of juvenile escapees have been periodically very high, and in some rivers in some years (many years in some cases), farmed escaped juveniles have even outnumbered wild juveniles (Carr & Whoriskey, 2006; Stokesbury & Lacroix, 1997; Stokesbury et al., 2001). There have been significant numbers of adult escapees found in the same rivers (Carr, Anderson et al., 1997).

2.2 | Do farmed escapees spawn in the wild?

While frequency varies in time and space, not all farmed salmon that escape from sea cages and thereafter enter rivers are sexually mature (Carr, Lacroix et al., 1997; Lacroix, Galloway, Knox, & MacLatchy, 1997; Madhun et al., 2015). Escapees may also ascend rivers outside the normal migratory times for wild salmon and even outside the spawning period. Indeed, triploid escapees, which are sterile, may enter freshwater albeit at a considerably reduced frequency compared to diploid escapees (Glover et al., 2015, 2016). In addition, not all male juveniles escaping to freshwater will become sexually mature as parr, especially because the tendency for parr maturation in farmed strains is lower than in wild populations (Debes & Hutchings, 2014; Einum & Fleming, 1997; Morris, Fraser, Eddington, & Hutchings, 2011; Yates, Debes, Fraser, & Hutchings, 2015). Therefore, not all escapees found in rivers will reproduce and hybridize with native fish.

Data from early surveys conducted in Norway revealed unweighted annual average maturation of escapes captured in rivers as 91.9% (range 77%–100% over the 12 years) and 86.8% (range 64%–100%) for males and females, respectively (Fiske et al., 2001). Also, in a recent study conducted in the River Namsen, middle Norway, most of the escapees entering the river were mature or maturing (Moe et al., 2016). In contrast, all of 29 small (0.4 kg) escapees captured in the River Steinsdalselva in western Norway in 2012 were immature (Madhun et al., 2015), and observations of large numbers of immature adults have been reported in rivers in Canada (Carr, Lacroix et al., 1997; Lacroix et al., 1997). Additionally, maturation status may differ between escapees captured in the very low reaches of rivers and river mouths, and further up in the system where spawning grounds typically occur. Despite the clear implications for patterns of introgression, maturation status, location of capture in the river and the life stage of escape are often poorly documented in monitoring programmes (Anon 2016).

Spawning of adult escapees has been reported in rivers in Scotland (Butler et al., 2005; Webb et al., 1991, 1993), Norway (Lura & Saegrov, 1991; Lura, Barlaup, & Saegrov, 1993; Saegrov, Hindar, Kalas, & Lura, 1997) Canada (Carr, Anderson et al., 1997) and outside the species' native range on the Pacific coast of North America (Volpe et al., 2000). These reports are based on visual observations and/or the analysis of diagnostic pigmentation in eggs that is derived from the commercial diet of the farmed fish, which not only permits validation of successful spawning but, also its quantification. In the River Vosso in western Norway for example, an estimated 81% of the redds dug in the autumn of 1995 were by farmed escaped females (Saegrov et al., 1997). In a study conducted across 16 rivers in the west and north of Scotland in 1991, farmed females were documented to spawn in 14 rivers with a mean of 5.1% of juveniles originating from farmed females (Webb et al., 1993). In the Magaguadavic River in Canada, from a total of 20 redds sampled in 1993, a minimum of 20% of the eggs deposited were from farmed females (Carr, Anderson et al., 1997).

On average, the relative spawning success of adult farmed salmon escapees is significantly lower than for wild salmon (Fleming et al., 2000; Fleming, Jonsson, Gross, & Lamberg, 1996; Weir, Hutchings, Fleming, & Einum, 2004). Based on studies conducted in seminatural spawning arenas, estimates of the spawning success of farmed escapees, in comparison with wild salmon, are ~1%–3% for males and ~30% for females, respectively (Fleming et al., 1996), although their relative success may vary and be case specific (Fleming et al., 1996, 2000; Weir et al., 2004). For example, adult farmed males attained a high of 24% success in the spawning arenas in Ims (Fleming et al., 2000). Comparative spawning studies between wild and farmed salmon have also been conducted in the wild, supporting the conclusion that farmed escapees are inferior competitors (Fleming et al., 2000). Studies have also shown that the relative spawning success of adult farmed escapees probably varies considerably with the life stage at which the fish escaped (Fleming, Lamberg, & Jonsson, 1997; Weir et al., 2004). It is likely that recently escaped adults that have compromised fin quality, body shape and swimming performance, are unlikely to compete as well as farmed salmon that have escaped in freshwater as juveniles or smolts, or post-smolts early in the marine rearing phase that have had the opportunity to develop a more wild-type body shape and behaviours during their longer exposure to natural conditions.

There are two highly significant implications from the results of the spawning studies. First, they imply that if there are 10% adult farmed escapees on the spawning grounds, their genetic contribution is likely to be significantly lower than 10% (although this will vary in time and space). Second, large and consistent differences in success between the sexes strongly indicate that the clear majority of the genetic contribution is likely to be from farmed females spawning with wild males, thus producing hybrids.

While farmed escapees may successfully spawn in the same areas of rivers as wild fish (Butler et al., 2005), studies have shown that adult farmed escapees do not necessarily use the same regions of a river during the spawning season as wild fish (Moe et al., 2016; Okland et al., 1995; Thorstad et al., 1998). Furthermore, in the absence of significant migration barriers such as large waterfalls, farmed escapees have a tendency to migrate to the upper reaches of rivers (Moe et al., 2016; Thorstad et al., 1998). In addition to area use differences, the timing of farmed salmon spawning may not be synchronized with the native population (Fleming et al., 2000; Moe et al., 2016; Saegrov et al., 1997; Webb et al., 1991). Variations in "time and space," in addition to the documented competitive inferiority of farmed escapees under spawning, may contribute to a partial or total miss-match of spawning relative to wild salmon under certain conditions and thereafter influence patterns of introgression and offspring survival.

The spawning success of escaped male farmed parr in the wild has not been investigated. However, wild male parr contribute significantly to breeding in native populations (Herbinger, O'Reilly, & Verspoor, 2006; Johnstone, O'Connell, Palstra, & Ruzzante, 2013; Taggart, McLaren, Hay, Webb, & Youngson, 2001), and in experimental studies, farmed male parr have been documented to successfully compete for and spawn with wild salmon (Garant, Fleming, Einum, & Bernatchez, 2003; Weir, Hutchings, Fleming, & Einum, 2005). Therefore, it is likely that they contribute to introgression, especially in rivers where large numbers of escaped juveniles occur (Carr & Whoriskey, 2006; Stokesbury & Lacroix, 1997; Stokesbury et al., 2001). Indeed, although not unequivocally demonstrated, an early study of introgression conducted in Ireland based on escapes of farmed parr into the river suggested that mature parr probably contributed to spawning (Clifford et al., 1998a).

Parr spawning is potentially of critical importance and may "fast track" introgression of farmed salmon in natural populations as the escapees do not have to survive until adulthood to spawn. The potential effect of this on introgression within wild populations has been highlighted based on modelling studies (Hindar, Fleming, McGinnity, & Diserud, 2006). However, the actual impact and relative spawning success for male parr of farmed, hybrid and wild origin is uncertain. One study observed a several fold higher spawning success of farmed male parr (Garant et al., 2003), while a similar study found smaller differences and a higher success of hybrid than either wild or farmed parr (Weir et al., 2005).

Sperm quality can influence the reproductive success of farmed escapees in the wild. Experimental studies have shown that there are significant differences in sperm morphology (Gage et al., 2004; Gage, Stockley, & Parker, 1998) and fertilization success among individual males (Gage et al., 2004). However, when farmed and wild salmon have been reared under identical conditions (Yeates, Einum, Fleming, Holt, & Gage, 2014), or taken directly from farms and from the wild (Camarillo-Sepulveda et al., 2016), no systematic differences in sperm and egg quality or *in vitro* fertilization success have been observed between farmed and wild salmon. This leads to the conclusion that if individual farmed escaped adults manage to partake in spawning in the wild, despite their general competitive inferiority, they will have similar fertilization success to wild adults.

Egg size is positively correlated with female size (Kazakov, 1981; Thorpe, Miles, & Keay, 1984), and when body size is adjusted for, farmed escapees display smaller eggs than wild salmon (Fleming et al., 2000; Lush et al., 2014; Srivastava & Brown, 1991). However, if the escapees entering the river are larger than the wild fish, as is sometimes the case, egg sizes of farmed offspring can be comparable to those of wild salmon (Solberg, Dyrhovden, Matre, & Glover, 2016; Solberg, Fjelldal, Nilsen, & Glover, 2014). In addition, the number of eggs per farmed female will be comparable to or greater than for wild fish. Egg size is important in early offspring survival in the wild, with larger eggs leading to larger offspring and higher survival (Einum & Fleming, 2000; Skaala et al., 2012).

3 | GENETICS

3.1 | What level of farmed salmon introgression has occurred in native populations?

Genetic changes in native populations because of farmed escaped salmon successfully spawning have been documented in several scientific studies stretching back to the early 1990s. The first documentation was obtained from the Glenarm River in Northern Ireland when a fish cage broke in the local bay in 1990 leading to a large intrusion of adult escapes (Crozier, 1993). By genotyping several allozymes, introgression of the farmed escaped salmon was documented. This was straightforward to demonstrate because the farmed salmon were of Norwegian origin and thus displayed fully diagnostic alleles at some of the loci compared to the wild Northern Irish population. Seven years later, the farm-diagnostic alleles were still present in juveniles sampled in the river, demonstrating the persistence of the non-native farmed fish in the population (Crozier, 2000). The author also observed a new non-native allele in the population that was not detected in the initial study, suggesting further introgression had occurred.

Two studies were conducted in NW Ireland in the 1990s. One of these used a combination of a semidiagnostic allele at a minisatellite locus, and a diagnostic haplotype in mitochondrial DNA (mtDNA), to identify introgression of farmed salmon in the local river that supported a hatchery facility for commercial farming of Norwegian salmon (Clifford et al., 1998a). These authors concluded that juveniles had escaped from the farm into the upper part of the river, smoltified, migrated to the sea and thereafter homed back to the site of escape to successfully interbreed with the wild population. Moreover, breeding of farmed males in the lower part of the river was also indicated, but this could have been due to mature farmed male parr that had moved downstream from the farm and successfully spawned together with the native population.

The next Irish study was conducted by the same research group and using the same genetic markers in two rivers in NW Ireland (Clifford et al., 1998b). Here, the authors were able to document the successful introgression of adult farmed salmon in two native populations studied in the period 1993–1995, as a result of larger individually reported escape events. Importantly, in both studies conducted by this group, the independent occurrence of the semi-diagnostic or diagnostic alleles in the juveniles captured in the river demonstrated that not only had the farmed fish successfully spawned, but they had hybridized with the local populations. Thus, already by the mid-1990s, cases of the successful genetic hybridization and introgression of juvenile and adult farmed escaped salmon in native populations had been documented, at least in Ireland and Northern Ireland where farmed salmon of non-native origin were reared.

The first genetic study to address introgression of farmed salmon in wild populations outside Ireland was conducted in Norway approximately a decade later (Skaala, Wennevik, & Glover, 2006). There are important differences between the studies in Ireland (including Northern Ireland) and Norway. The first is that the Norwegian study was conducted one to two decades after farmed escaped salmon had been observed in high frequencies on the spawning grounds of some of the rivers investigated (Fiske et al., 2006; Gausen & Moen, 1991; Saegrov et al., 1997). This posed two challenges. It meant that the study investigated long-term and cumulative introgression of farmed salmon rather than a well-defined or a single escape episode. Also, it meant that historical fish scale samples, collected from angling, were required to recreate the genetic structure of the populations prior to or in the early stages of farming to assess genetic changes. The authors genotyped temporal samples for seven populations using microsatellite markers, an approach that had been previously (Nielsen, Hansen, & Loeschcke, 1997) and subsequently (Nielsen & Hansen, 2008) demonstrated as an effective way to investigate temporal genetic stability in populations in the face of anthropogenic challenges.

The second key difference between the early Irish and first Norwegian studies was the genetic power of the molecular markers used. The early Irish studies exploited fixed or almost fixed allele differences between the Norwegian farmed salmon being reared in the region and the local wild population(s). However, Norwegian farmed salmon originate from a diverse range of Norwegian wild populations (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991) such that the allele frequencies of Norwegian farmed strains overlap with wild Norwegian populations for several classes of genetic markers (Karlsson, Moen, Lien, Glover, & Hindar, 2011; Skaala, Hoyheim, Glover, & Dahle, 2004; Skaala, Taggart, & Gunnes, 2005). This presents significant statistical challenges to identify and quantify introgression in wild Norwegian populations, especially when gene flow over time arises from multiple farmed strains (Besnier, Glover, & Skaala, 2011).

Despite these analytical challenges, the first Norwegian study detected temporal genetic changes in some of the populations investigated (Skaala et al., 2006). These authors suggested that introgression of farmed escaped salmon was the primary cause of the changes. This was based on the high frequencies of escapees on the spawning ground of these rivers, and increased allelic diversity in some of the populations. At the same time, a loss in genetic diversity among wild populations between the historical and contemporary samples was observed.

The study of Skaala and colleagues (2006) was later expanded upon. Using 22 microsatellite markers, a spatio-temporal analysis of genetic structure across 21 populations covering the entire Norwegian coastline was examined using archived samples from as far back as the 1970s (Glover et al., 2012). Temporal genetic changes were observed in some wild populations, while not in others. The study also considered the among-population patterns of introgression, and why it occurred in some rivers, but not in others with apparently similar frequencies of farmed escapees over the same period. The authors suggested that the density of the native population was probably a major factor modifying the level of introgression, via spawning (Fleming et al., 1996) and thereafter, juvenile competition (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012). This mechanism has also been observed in other species where deliberate releases of hatchery fish and the level of admixture in the recipient population were suggested to be linked with density and thus resilience of the native population (Hansen & Mensberg, 2009).

The second Norwegian study (Glover et al., 2012) of farmed salmon introgression also demonstrated a decrease in among-population genetic structure over time. This was especially noticeable among populations which displayed the strongest temporal changes. Notably, all the temporally unstable populations gained new alleles with time. The potential loss of genetic diversity among wild populations following introgression of farmed salmon escapees had been earlier hypothesized (Mork, 1991) as farmed salmon have a limited genetic background (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991). Finally, through simulations using the observed effective population sizes, the authors excluded genetic drift as a major contributory factor of the observed temporal genetic changes in those populations and, thus, concluded that introgression of farmed escapees was the primary driver of the observed temporal genetic changes.

Using a 7K single nucleotide polymorphism (SNP) chip, a panel of SNP markers have been identified that permit the differentiation of farmed Norwegian salmon and wild Norwegian salmon, irrespective of the origin of the domesticated strain or the wild population (Karlsson et al., 2011). These markers circumvent the statistical challenge where gene flow from multiple farmed strains tends to cancel each other out (Besnier et al., 2011). Using these collectively informative SNP markers, a reference panel of Norwegian farmed salmon, historical and contemporary samples from 20 wild salmon populations distributed throughout Norway, and approximate Bayesian computation-based estimates, the first estimation of cumulative gene flow from farmed salmon to wild salmon was produced (Glover et al., 2013). These authors estimated that over the period of the study (three to four decades), introgression of farmed salmon ranged from 0% to 47% per population, with a median of 9.1%. This represented an important quantum-step in knowledge, as it provided the first empirical evidence for Challenge 1 (Figure 3), which is a key step in quantifying and understanding the potential genetic effect of farmed escapees on wild populations. Glover et al. (2013) demonstrated that the observed frequency of escapees in rivers was a significant but not the only driving force explaining interpopulation introgression levels. The results obtained supported earlier suggestions that the density of the native population played a major role in influencing introgression success of farmed salmon (Glover et al., 2012). This conclusion was further supported in a subsequent modelling study that related introgression rates and observed incidence of escapees in the rivers studied (Heino, Svåsand, Wennevik, & Glover, 2015).

The most recent and extensive investigation of introgression was conducted in 147 Norwegian salmon rivers, representing three-quarters of wild salmon spawners in Norway (Karlsson, Diserud, Fiske, & Hindar, 2016). Their approach used the panel of SNPs developed for identification of farmed and wild salmon (Karlsson et al., 2011) and a recently developed statistical approach to estimate the proportion of the wild genome *P(wild)* remaining (Karlsson, Diserud, Moen, & Hindar, 2014). This statistical approach has the advantage that it can be used to compute individual fish admixtures, in addition to the fact that it does not require a historical baseline, which was a requirement of the methodology implemented in Glover et al. (2013). Karlsson et al. (2016) found statistically significant introgression in half of the wild populations studied and levels of introgression above 10% in 27 of 109 rivers represented by modern adult samples. Overall, they reported a mean and median introgression rate of 6.4 and 2.3%, respectively, in 109 populations with a contemporary adult sample of 20 fish or more. These authors also reported a correlation between incidence of escapees in the rivers and introgression levels, supporting earlier observations across 20 Norwegian populations (Glover et al., 2013).

Studies of introgression in other regions are more limited. The analysis of microsatellites in a recent study of a small coastal stream in western Scotland (Verspoor et al., 2016) found no detectable evidence for introgression despite being in the centre of a marine production area and the catchment being used for freshwater cage rearing of farm smolts. However, the power of the analysis to be informative was constrained by the historical data and sample sizes. In contrast, an earlier study documented European ancestry among farmed escaped salmon in the Chamcook Stream and the Magaguadavic River, New Brunswick, Atlantic Canada, despite the fact that farming salmon of European ancestry has never been permitted in this region (O'Reilly et al., 2006). Some evidence has also been reported of genetic variation in the Penobscot River that is typically only found in salmon of European ancestry (Lage & Kornfield, 2006). The only published study investigating genetic changes in native populations in this region was conducted on the Magaguadavic River where juvenile and adult escapees had been observed among the wild spawners over a period of approximately 20 years (Carr & Whoriskey, 2006; Carr, Anderson et al., 1997). The combined analysis of microsatellites and SNPs revealed temporal genetic changes in the population in the period

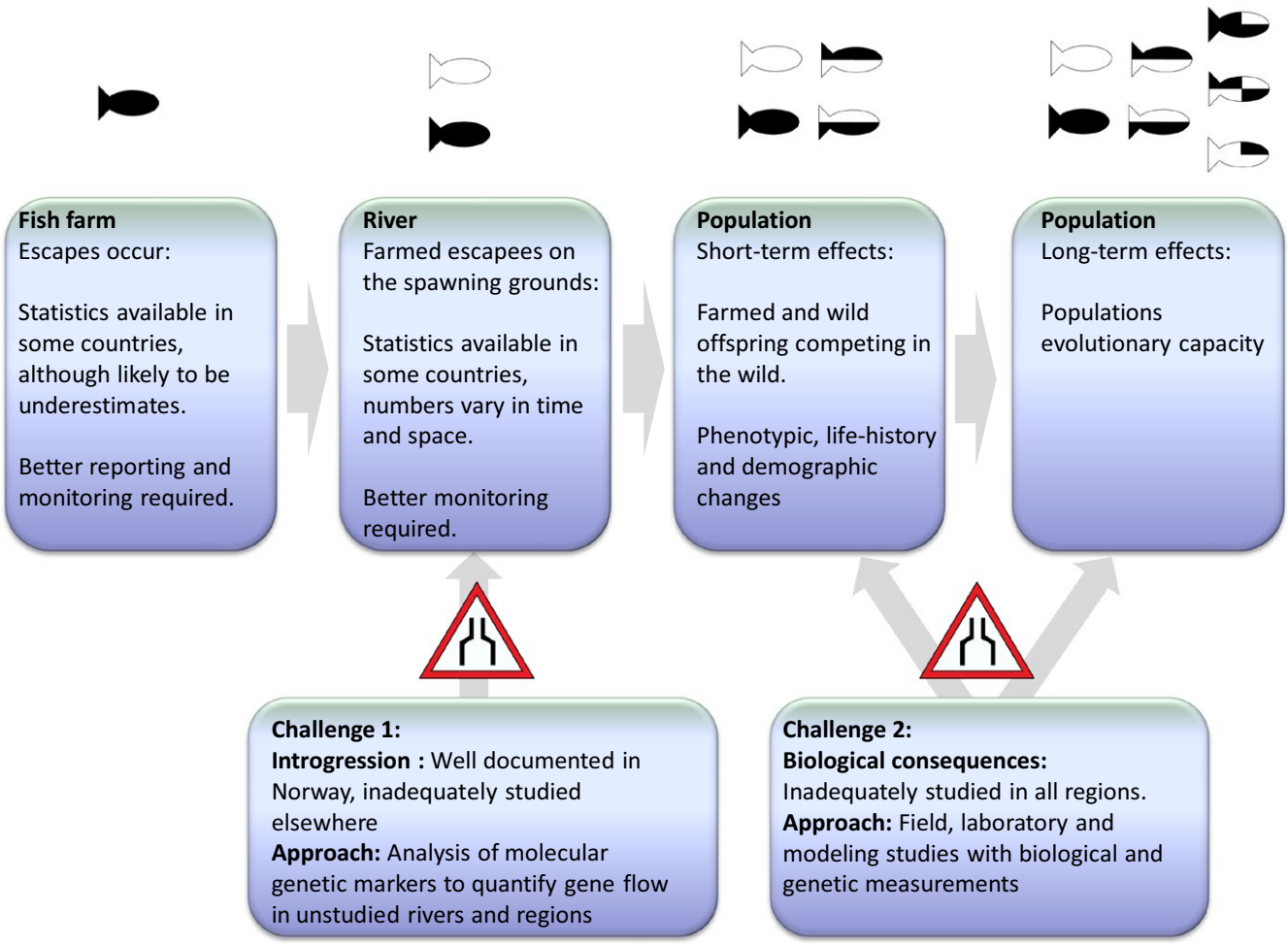

FIGURE 3 The two major challenges limiting current documentation of genetic impact of farmed escaped Atlantic salmon on wild populations. It is important to note that challenge 1 has recently been addressed in ~150 Norwegian rivers (Glover et al., 2013; Karlsson et al., 2016), but challenge 2 remains more or less completely unaddressed

1980 to 2002 and simultaneously demonstrated that the wild population had become more similar to samples of farmed fish in the region with time (Bourret, O'Reilly, Carr, Berg, & Bernatchez, 2011). These authors also observed an increase in linkage disequilibrium (LD) with time, but no drop in allelic diversity was observed, even though the population displayed a near total collapse in adult spawners during this period. This last observation parallels the observations, for example, in the River Vosso in Norway which displayed a population collapse but retained significant allelic diversity due to farmed salmon introgression (Glover et al., 2012).

3.2 | Is the Atlantic salmon domesticated?

Farmed salmon is regarded as one of the most domesticated fish species farmed for food (Teletchea & Fontaine, 2014) and was the first to be subject to a systematic family-based selective breeding programme (Gjedrem, 2010). The world's first commercial salmon breeding programme was initiated in Norway in the period 1971–1974 when gametes from mature adult salmon from one Swedish and 40 Norwegian rivers were collected and transferred to the Sundalsøra research facilities of the Agricultural University of Norway (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991). These fish formed four genetically distinct substrains (Gjoen & Bentsen, 1997; Skaala et al., 2004) each with a four-year generation time, that were subject to a combination of within- and among-family selection for commercially important traits. These four initial substrains form the basis of the genetic material now produced by Aqua-Gen and have arguably the best documented genetic backgrounds that are publicly available (Gjedrem, 2000, 2010; Gjedrem, Gjoen et al., 1991). Other local strains of farmed salmon, based on either single or multiple local river stocks, were also established in Norway in the early days of the aquaculture industry. These include the Mowi and Rauma strains owned by Marine Harvest and SalMar, respectively. They also include other strains, for example Jakta and Bolaks, which have been merged into what now forms the basis of the breeding company SalmoBreed. The three primary Norwegian strains (Aqua-Gen, SalmoBreed and Mowi–Marine Harvest) dominate global production of salmon, although their frequency of use varies greatly from country to country. For example in Atlantic Canada, only the St. John River domesticated strain (Friars, Bailey, & Oflynn, 1995; Quinton, McMillan, & Glebe, 2005; Wolters, Barrows, Burr, & Hardy,

2009) is permitted for use in commercial aquaculture, while in Scotland, some local-based strains, for example Landcatch, are also being used in addition to Norwegian strains (Powell, White, Guy, & Brotherstone, 2008; Tsai, Hamilton, Guy et al., 2015). Other strains under selection are also in existence in other countries, such as Tasmania, Australia (Taylor, Kube, Muller, & Elliott, 2009; Taylor, Wynne, Kube, & Elliott, 2007) and Chile (Lhorente, Gallardo, Villanueva, Carabano, & Neira, 2014; Yanez et al., 2014).

The first breeding programme, that ultimately ended up as forming the basis of the commercial strain now commonly known as Aqua-Gen, concentrated on improving growth rates and body size from 1972 onwards (Gjedrem, 2000, 2010; Gjedrem, Gjoen et al., 1991). Thereafter, this programme included other traits of commercial importance, such as age of sexual maturation from 1980, furunculosis susceptibility from 1989, fat content and fillet colour in 1990 and susceptibility to infectious salmon anaemia from 1992 (Gjedrem, 2000, 2010). Inclusion of these traits in the breeding programme occurred in parallel to a suite of genetic studies that demonstrated significant heritability estimates for relevant traits: body weight (Gjerde & Gjedrem, 1984; Gunnes & Gjedrem, 1978); susceptibility to mortality associated with vibriosis infection (Gjedrem & Aulstad, 1974); and smoltification rates (Refstie, Steine, & Gjedrem, 1977).

Subsequent studies of heritability in these and other strains of farmed salmon have supported early findings, and estimates of heritability for additional traits such as survival during early life (Rye, Lillevik, & Gjerde, 1990), sea age of sexual maturation (Gjerde, Simianer, & Refstie, 1994), susceptibility to furunculosis (Gjedrem, Salte, & Gjoen, 1991), susceptibility to sea lice (Glover, Aasmundstad, Nilsen, Storset, & Skaala, 2005; Kolstad, Heuch, Gjerde, Gjedrem, & Salte, 2005; Mustafa & MacKinnon, 1999; Yanez et al., 2014) and susceptibility to amoebic gill disease (Taylor et al., 2007, 2009) have been reported. Many of these traits have been included in breeding programmes, although this varies between programmes and regions. Today, the oldest breeding programmes have advanced to 12+ generations, and in 2005, Aqua-Gen changed from the traditional four-year generation time to a three-year generation time to increase the rate of genetic gain. In addition, some of the strains have been separated into distinct lines, while others compressed from multiple into single strains. The genetic gains from these breeding programmes have been remarkable and are addressed in the following chapter.

Recent developments in genomic tools and their application in animal breeding have opened new opportunities to understand the underlying genetic basis of commercially important traits and how to exploit them in breeding programmes. For example, QTLs (quantitative trait loci) have been identified and validated for a variety of traits including growth (Baranski, Moen, & Vage, 2010; Tsai, Hamilton, Guy et al., 2015; Tsai, Hamilton, Tinch et al., 2015), susceptibility to pancreatic disease (Gonen et al., 2015), susceptibility to infectious pancreatic necrosis (Houston et al., 2010; Moen, Baranski, Sonesson, & Kjoglum, 2009) and survival in the wild (Besnier et al., 2015). Furthermore, genomewide association studies identified single genes that influence important phenotypes, such as the *vgll3* locus acting on age of maturation in adult salmon (Ayllon et al., 2015; Barson et al., 2015). This gene could represent an effective target of selection to inhibit early maturation during the marine phase of the rearing cycle, which is especially problematic in males when not hindered through effective light treatment (Taranger et al., 2010). As a result of the above developments, and helped by the development of advanced genomic resources for the salmon (Houston et al., 2014; Lien et al., 2016; Tsai et al., 2016), QTL and genome-based selection is now being utilized in several of the commercial breeding programmes. It is likely that within the coming years, genome-based selection will become standard within salmon breeding. This is likely to increase the number of traits that can be selected for and the rate of genetic gain. In turn, these developments will lead to further genetic divergence from wild salmon.

3.3 | What genetic differences exist between wild and farmed salmon?

There are four primary reasons why farmed salmon are genetically different to wild salmon: 1. directional selection for commercially important traits within breeding programmes (which changes both target traits and any others which may be subject to hitch-hiking/coselection); 2. domestication selection (inadvertent genetic changes associated with general adaptation to the human-controlled environment and its associated reduction in natural selection pressure, as well as trait shifts due to trade-offs); 3. random genetic changes during domestication (initially founder effects and thereafter genetic drift across generations); 4. ancestry differences as farmed salmon may be of non-local or mixed-origin (Ferguson et al., 2007).

Currently, the only direct method of examining quantitative-genetic differences among wild, farmed and hybrid salmon is to carry out common-garden experiments, where fish are reared in a communal environment. As environmental variability is minimal or eliminated, any differences between the genetic groups, with the exception of maternal and potential epigenetic effects, will reflect genetic differences (although, depending on the experimental environmental conditions, cryptic genetic variation may not be detectable (Ghalambor, McKay, Carroll, & Reznick, 2007)). Multiple experimental approaches to elucidate and quantify the genetic differences between farmed and wild salmon have been implemented. Broadly, these approaches can be grouped into the following categories: analysis of molecular-genetic polymorphisms (Table 1), analysis of gene-transcription profiles (Table 2), comparative studies of genetic-based phenotypic response(s) under controlled hatchery or net pen conditions (Tables 3–8) and seminatural conditions (Table 9) and finally experimental comparisons in the natural environment (section below).

There are several key elements which provide significant challenges to conduct comparative experiments to quantify the genetic differences between farmed and wild salmon. First, many of the farmed strains now in existence were founded using brood fish collected from multiple wild populations or were subsequently mixed with other farmed strains at some stage of strain development. Thus, due to the fact that genetic differences in a wide range of traits are also observed among wild populations (Garcia de Leaniz et al., 2007; Taylor, 1991), it may be difficult to disentangle the relative influence

TABLE 1 Studies of molecular marker variation within and among farmed and wild salmon strains

Marker	Primary observation	Reference
20 enzymes	Comparison: 11 hatchery groups vs. 7 wild rivers. Heterozygosity: F < W Magnitude of difference = 26%	(Verspoor, 1988)
6 enzymes	Comparison: 5 Scottish and/or Norwegian farmed strains vs. 9 wild Irish populations. Heterozygosity & number of alleles: F < W (80%, comparisons including fixation of some loci)	(Cross & Challanain, 1991)
6 enzymes	Comparison: 9 Scottish and 7 Norwegian farmed strains vs. 18 Scottish wild populations. Heterozygosity F ≈ W. All farmed strains differed from their wild source populations and were on the same order as between wild populations	(Youngson, Martin, Jordan, & Verspoor, 1991)
12 enzymes, 3 single locus markers, 1 minisat	Comparison: 1 farmed strain and 2 wild populations. Genetic variation: F < W for multiple marker systems	(Mjolnerod et al., 1997)
Minisatellites	Comparison: Norwegian Mowi vs. Irish wild. Heterozygosity and number of alleles: F < W. Magnitude of difference = 53% and 56%, respectively	(Clifford et al., 1998b; Clifford, 1996)
15 microsatellites	Comparison: 3 farmed strains vs. 4 wild populations (Irish and Norwegian). Allelic diversity: F < W. Heterozygosity: F ≈ W	(Norris et al., 1999)
12 microsatellites	Comparison: 5 major farmed strains vs. 4 wild Norwegian populations. Allelic richness: F < W. Magnitude of difference = 58%. Genetic distances among farmed strains 2–8 × higher than between wild populations	(Skaala et al., 2004)
8 enzymes	Comparison: 5 major farmed strains vs. 4 wild Norwegian populations. Heterozygosity, # alleles, & polymorphic loci: F < W. Magnitude of differences = 12%–17%	(Skaala et al., 2005)
16 microsatellites, 26 SNPs	Comparison: 2 farmed strains vs. 5 wild populations (Norway & Scotland). An AquaGen strain expressed the highest degree of heterozygosity for both microsatellites and SNPs, while the highest allelic diversity was found in two wild populations	(Rengmark, Slettan, Skaala, Lie, & Lingaas, 2006)
12 microsatellites, 19 SNPs in mtDNA	Comparison: 4 Norwegian farmed strains vs. 4 Norwegian wild populations. Microsatellites—allelic richness & heterozygosity: F < W. MtDNA variability: F > W	(Karlsson et al., 2010)
112 SNPs, 8 microsatellites	Comparison: Farmed and wild-caught salmon from Magaguadavic River, Canada. A SNP marker differed between the two groups and was closely associated with parr marks	(Bourret et al., 2011)
7000 SNPs	Comparison: 13 Norwegian wild and 12 Norwegian farmed strains. 60 collectively diagnostic SNPs identified all farmed, wild and *in silico* F1 hybrids	(Karlsson et al., 2011)
261 SNPs, 70 microsatellites	Comparison: Three independent domesticated/captive strains and their wild progenitors. Genetic diversity: D ≈ W, and in one comparison D > W	(Vasemagi et al., 2012)
5650 SNPs, resulting in 2797 to 4733 polymorphic markers pr. Strain	Comparison: Same as Vasemagi et al., 2012;. Heterozygosity: Mixed evidence (D < W, W < D, D ≈ W). Few genomic regions under selection and not consistently identified in all comparisons	(Makinen et al., 2015)
7000 SNPs	Comparison: Cermaq strain vs. four Norwegian populations. 44 loci under selection, linked to molecular functions associated with domestication-related traits	(Gutierrez et al., 2016)

Note: Comparisons in genetic diversity when a sample(s) from a random fish cage as opposed to the main strain(s) itself has been used to compare to a wild population has not been included in the above table. This is because a cage on a commercial farm typically contains fish resulting from a low or relatively low number of families and does therefore not accurately represent the genetic diversity nor allele frequencies of the actual farmed strain itself. The reader is referred to the following publications for data related to variation in allele profiles between cages on and among fish farms (Glover et al., 2008; Glover, Hansen, & Skaala, 2009; Glover, Skaala, Sovik, & Helle, 2011; Zhang et al., 2013). F, farm, W, wild, D, domesticated (combination of farmed and hatchery-reared fish).

TABLE 2 Common-garden comparisons of gene-transcription profiles in farmed and wild salmon under controlled hatchery conditions

Tissue	Life stage/tissue	Primary observation	Matched	Reference
Whole fry	Yolk-sac resorption	1.4%–1.7% of genes investigated: F ≠ W. Magnitude of difference: 18%–25%	Age, stage	(Roberge et al., 2006)
Whole fry	Yolk-sac resorption	6% of genes investigated: BC ≠ W Magnitude of difference: 76%	Age, stage	(Roberge et al., 2008)
Liver	Fry	32–39 transcripts: F ≠ W 23–26 transcripts: BC ≠ W 11–53 transcripts: F ≠ BC	Age	(Normandeau et al., 2009)
Gill	Mature males	2.3% (67 genes) of genes investigated: F ≠ H ≠ W Genes related to energy metabolism and immunity altered	Age, stage	(Debes et al., 2012)
Whole fry	Yolk-sac fry	mRNA translation-related pathways: F > W Nervous and immune system related pathways: F < W	Age, stage	(Bicskei et al., 2014)
Whole fry	Feeding fry	Digestive and endocrine activities, carbohydrate, energy, amino acid and lipid metabolism pathways: F > W Environmental information processing and immune system pathway: F < W	Age, stage	(Bicskei et al., 2014)
Eggs	Eyed-eggs	ECM receptor interactions pathways: F < W Genetic information processing and metabolism pathways: F > W Additive, maternal dominance and overdominance inheritance	Age, stage	(Bicskei et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

of domestication (in its broad sense) from origin-based (i.e. ancestry) population-specific differences.

One way to circumvent this challenge is to use a farmed strain that is known to be based on a single or low number of wild populations, either from the onset of domestication (Debes & Hutchings, 2014; Solberg et al., 2014), or by altered strain contributions through the first generations of domestication (Einum & Fleming, 1997). An alternative is to include multiple farmed strains and/or wild populations to identify evidence of parallel evolution. While the former has been done in several studies (Debes & Hutchings, 2014; Einum & Fleming, 1997; Fleming, Agustsson, Finstad, Johnsson, & Bjornsson, 2002; Solberg et al., 2014; Thodesen, Grisdale-Helland, Helland, & Gjerde, 1999), the latter is more resource demanding, although it has been carried out for several common-garden studies (Fraser, Cook, Eddington, Bentzen, & Hutchings, 2008; Glover, Hamre, Skaala, & Nilsen, 2004; Harvey, Glover, Taylor, Creer, & Carvalho, 2016; Normandeau, Hutchings, Fraser, & Bernatchez, 2009; Solberg et al., 2016) and for studies of polymorphic genetic markers (Karlsson, Moen, & Hindar, 2010; Norris, Bradley, & Cunningham, 1999; Skaala et al., 2004). In addition, a few studies have combined both approaches by comparing multiple farmed and/or wild strains, while also including the major wild founding population (Harvey, Glover et al., 2016; Neregard et al., 2008; Solberg et al., 2016).

A second key challenge in attempting to identify genetic differences between farmed and wild salmon is when the traits under study are correlated with fish size, growth rate or developmental timing. This represents a challenge because the offspring of farmed salmon display higher growth rates than wild salmon, will therefore outgrow the wild fish during an experiment, be larger than the wild fish upon initiation of certain types of experiments or may reach certain life stages at an earlier age. This may result in challenges to disentangle cause and effect on the target trait. To make comparisons, one can select the smallest farmed fish and largest wild fish to create overlapping size distributions but at the cost of random sampling (Fleming & Einum, 1997; Fleming et al., 2002; Morris et al., 2011). One can also undertake a time-staggered experiment so that all groups are of the same size or developmental stage without having to sort the fish subsequently (Thodesen et al., 1999; Zhang et al., 2016) (even though this may in turn cause developmental and/or environmental-related differences due to varying age at size, or age at stage). One can also compensate or account for variations in body size in the data analyses (Debes & Hutchings, 2014; Glover et al., 2004), manipulate growth of the farmed or wild salmon by changing temperature and or feed rations or use a combination of approaches such as investigating both size-matched individuals and age-matched individuals to reduce potential bias (as has been made in the case of a rainbow trout (*Oncorhynchus mykiss*, Salmonidae) domestication study) (White, Sakhrani, Danzmann, & Devlin, 2013). Alternatively, experiments can be conducted on the very early life-history stages (Bicskei, Bron, Glover, & Taggart, 2014; Debes, Fraser, McBride, & Hutchings, 2013; Fraser, Minto, Calvert, Eddington, & Hutchings, 2010; Solberg et al., 2014) before intrinsic growth differences lead to differences in size. However, while the latter represents the most "unbiased approach," it obviously limits measurements to early life-history stages.

Another significant challenge in disentangling the genetic differences between wild and farmed salmon is that among-family variation within strains is typically large (Harvey, Glover et al., 2016; Reed et al., 2015; Skaala et al., 2012; Solberg et al., 2016; Solberg, Glover, Nilsen, & Skaala, 2013; Solberg, Zhang, Nilsen, & Glover, 2013). Overlooking

TABLE 3 Common-garden comparisons of growth-related traits of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Growth/body weight	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F ≥ W, intraspecific ≠ interspecific competition	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 1+	F > W	Age	(Fleming & Einum, 1997)
	Salt water, smolt 1+ and 2+	F > W	Stage	(Thodesen et al., 1999)
	Freshwater, 1+ and 2+ Salt water, 2+	Freshwater: F = W Salt water: F > W	Size (1+), Age	(Fleming et al., 2002)
	Salt water, smolt 1+	F = W (1 month after seawater transfer) F > W (>1 month after seawater transfer)	Size, Age	(Handeland, Bjornsson, Arnesen, & Stefansson, 2003)
	Freshwater, adult 3+	F > W	Age	(Dunmall & Schreer, 2003)
	Freshwater and salt water, 1+ and 2+	F > H > W	Age	(Glover & Skaala, 2006)
	Freshwater, 1+	F > H > W	Age	(Glover, Bergh et al., 2006)
	Freshwater, 1+	F > H > W	Age	(Glover, Skar et al., 2006)
	Fresh and salt water, 0+, 1+ and 2+	F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 1+	F > W	Size, Age	(Wolters et al., 2009)
	Freshwater, 1+	BC ≥ W	Age	(Darwish & Hutchings, 2009)
	Freshwater, 2+	F > H (F1,F2,BC) > W	Age	(Fraser, Houde et al., 2010)
	Freshwater, 1+	F > H (F1,F2,BC) > W	Size, Age	(Morris et al., 2011)
	Freshwater, 0+	F > W	Age	(Solberg, Glover et al., 2013)
	Freshwater, 0+ and 1+	F > W, intraspecific = interspecific competition	Age	(Solberg, Zhang et al., 2013)
	Fresh and brackish water, 2+ and 3+	F > F2 > F1 > BC > W	Age	(Debes et al., 2014)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Solberg et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Glover et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Juleff et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Solberg et al., 2016)
Endocrine growth regulation	Freshwater, 1+ and 2+ Salt water, 2+	Pituitary and plasma GH[a]: F > W Plasma IGF-1[b]: F = W	Size (1+), Age	(Fleming et al., 2002)
	Salt water, smolt 1+	Plasma GH levels: F = W	Size, Age	(Handeland et al., 2003)
	Freshwater, 0+ (liver)	GH treatment: Growth response: F < W Plasma GH and IGF-1: F = W IGF-1 and GHR[c] mRNA levels: F = W	Size, Age	(Neregard et al., 2008)
	Freshwater, 0+ (head kidney)	IGF-1 mRNA levels: F > W	Age	(Solberg, Kvamme, Nilsen, & Glover, 2012)
Feed intake and utilization	Salt water, smolt 1 + and 2+	Relative feed intake: F > W Feed efficiency ratio (FER): F > W	Stage	(Thodesen et al., 1999)
	Salt water, smolt 1+	Relative feed intake: F = W Feed efficiency ratio (FER): F > W	Size, Age	(Handeland et al., 2003)
	Freshwater, 1+	Relative feed intake: F > W Feed conversion ratio (FER): F = W	Age	(Wolters et al., 2009)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.
[a]Growth hormone, [b]insulin-like growth factor, [c]Growth hormone receptor.

family variation may lead to erroneous conclusions regarding the degree of genetic differentiation between farmed and wild salmon. Large-scale experiments using thousands of experimental animals, where both the within-strain family variation and the interstrain differences are investigated, represent the most robust analysis (Solberg et al., 2014; Solberg, Glover et al., 2013; Solberg, Zhang et al., 2013).

TABLE 4 Common-garden comparisons of life stage development of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Embryonic development	Egg + yolk-sac fry	Days to 50% hatch: BC< or >W Length at hatch: BC = W	Age	(Darwish & Hutchings, 2009)
	Egg	Degree days to hatch: F > H (F1,F2,BC) > W	Age	(Fraser, Minto et al., 2010)
	Yolk-sac fry	Length at hatch: F ≥ H (F1,F2,BC) ≥ W Length at first feeding: F ≥ H (F1,F2,BC) ≥ W Yolk-sac conversion efficiency: F ≤ H (F1,F2,BC) ≤ W	Age	(Fraser, Houde et al., 2010)
	Egg + yolk-sac fry	Degree days to hatch: F = H (F1,F2,F3,BC) = W Yolk-sac conversion efficiency: F = H (F1,F2,F3,BC) = W Length at first feeding: F > H (F1,F2,F3,BC) > W	Age	(Debes et al., 2013)
	Egg + yolk-sac fry	Degree days to hatch: F > H > W Length at yolk-sac absorption: F = H = W	Age	(Solberg et al., 2014)
Parr maturation	Freshwater, 0+	Maturation rate: F < W	Age	(Fleming & Einum, 1997)
	Freshwater, 1+	Maturation rate: F < F1 < F2 < W < BC	Size, Age	(Morris et al., 2011)
	Freshwater, 0+	Maturation rate: F1 < BC < W	Age	(Yates et al., 2015)
Smolting	Freshwater, 1+	Smolting rate: F > W	Age	(Fleming & Einum, 1997)
	Freshwater, 1+	Smolting rate: F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 2+	Smolting rate: F > H (F1,F2,BC) > W	Age	(Fraser, Houde et al., 2010)
Adult maturation	Salt water, 1SW	Maturation: F < H < W (only ♂ in F, only ♀ in W)	Age	(Glover, Ottera et al., 2009)
	Fresh and salt water, post-smolt	Maturation rate: F < W (♀ < ♂ in F, ♀ = ♂ in W). ♂: F > H (F1,F2,BC), ♀: F < H (F1,F2,BC)	Age, Stage	(Debes et al., 2014)
Reproduction	Freshwater, gametes	Sperm form, function, N and competitiveness: F = W Egg and sperm fertility: F = W Egg–sperm compatibility: F = W	Age	(Yeates et al., 2014)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 5 Common-garden comparisons of behavioural traits of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Aggression	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F > W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 0+	F ≥ W, F1 > W, BC ≥ W	Size	(Houde et al., 2010a)
Dominance	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F ≤ W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 0+	When given no prior residency: F > W When F given prior residency: F > W When W given prior residency: F < W	Age	(Metcalfe et al., 2003)
Antipredator behaviour	Freshwater, 0+	Refuge time: F < W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	Response time: F = W Refuge time: F < W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 1+ and 2+	Flight and heart response: F < W (1+), F = W (2+)	Size, Age	(Johnsson, Hojesjo, & Fleming, 2001)
	Freshwater, 0+	Refuge time after simulated attack: F < H < W F1, F2, BC < W	Age	(Houde et al., 2010b)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 6 Common-garden comparisons of plasticity (reaction norms) in farmed and wild salmon under controlled hatchery conditions

Variable	Life stage/tissue	Primary observation	Matched	Reference
Temperature	Freshwater, 0+	Effect on growth: F = W	Size, Age	(Fleming & Einum, 1997)
	Salt water, smolt	Mortality after exposure to cold temperatures: F = H = W	Age	(Hamoutene, Costa, Burt, Lush, & Caines, 2015)
	Freshwater, 0+	Cold temperature effect on early survival F = W Cold temperature effect on early growth F ≠ W	Age	(Solberg et al., 2016)
	Freshwater, 0+	Effect on growth F ≠ W	Age	(Harvey, Glover et al., 2016)
	Freshwater, 0+	Effect on survival to hatch and length at hatch: BC = W Effect on time to 50% hatch: BC ≠ W Effect on post-feeding growth: BC = W	Age	(Darwish & Hutchings, 2009)
	Freshwater, 0+	Effect on growth: F1 ≈ BC ≈ W Effect on parr maturation: F1 = BC = W	Age	(Yates et al., 2015)
Acid tolerance	Freshwater, 0+ (alevins + parr)	Effect on mortality: F or F1 H ≥ W, F2 H ≤ W	Age	(Fraser et al., 2008)
Salinity	Salt water, smolt 1+	Mortality following seawater transfer: F > W	Size, Age	(Handeland et al., 2003)
	Fresh and salt water, post-smolt	Effects on growth rate: F ≠ H (F1,F2,BC) ≠ W	Age, Stage	(Debes et al., 2014)
	Salt water, smolt	Mortality following seawater transfer: F = H = W	Age	(Hamoutene et al., 2015)
Sediments	Salt water, 1 SW	Transcriptional plasticity: F = H = W	Age	(Debes et al., 2012)
	Fresh and salt water, post-smolt	Effect on growth reduction: F = H (F1 = F2 = BC) = W	Age, Stage	(Debes et al., 2014)
Environmental stress	Freshwater, 0+	Stress induced growth reduction: F < W	Age	(Solberg, Glover et al., 2013)
Nutrition levels	Freshwater, 1+	Compensatory growth after food limitations: F = H (F1,F2,BC) = W	Size	(Morris et al., 2011)
	Freshwater, 0+	Growth reduction at restricted rations: F > W	Age	(Solberg, Zhang et al., 2013)
	Freshwater, 0+	Effect of varying feed availability on growth: F = H = W	Age	(Harvey, Solberg et al., 2016)
Density	Freshwater, 0+	Effect on growth: F = H = W	Age	(Harvey, Juleff et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

However, such experiments are resource demanding, and where extensive physiological, observational or other measurements are involved, such extensive sampling is rarely feasible.

Not all experiments comparing farmed and wild salmon have effectively dealt with the above-mentioned challenges, and as such, results should be interpreted critically. Nevertheless, a growing body of literature addressing this topic is now published, unveiling a comprehensive list of genetic-based differences between farmed and wild salmon (Tables 2–9). Some of the most important and extensive differences between these groups are discussed below.

3.3.1 | Studies of molecular-genetic markers

Analysis of assumed selectively neutral, or close to selectively neutral, molecular-genetic markers in farmed strains and wild populations simultaneously can provide information about the levels of genetic diversity within (including potential inbreeding) and among the strains and populations. Where farmed strains are based on a single wild population (which is less often), it can also quantify genetic divergence that may have occurred due to neutral processes such as founder effects and genetic drift. Most studies investigating allelic variation in farmed strains and wild populations have clearly demonstrated reduced genetic diversity (measured primarily as a reduction in the number of alleles but also as a reduction in heterozygosity in some studies) in farmed strains either in relation to their wild donor populations, or in relation to other wild populations chosen for the comparison (Table 1). This is consistent with the finite number of breeding adults used in each strain, and the inevitable consequences this has on the rate of inbreeding.

Highly polymorphic markers with large numbers of alleles, such as microsatellites, are highly sensitive to changes in genetic variation. This is because they often display many alleles that are typically

TABLE 7 Common-garden comparisons of morphology and physiology of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
External morphology	Freshwater, 0+	F ≠ W in 13 of 28 traits. F more robust, deeper, bodies and smaller rayed fins than W	Age	(Fleming & Einum, 1997)
Various commercial traits	Salt water, adult (full commercial cycle)	Fat content: F = W Skin coloration: F = W Flesh texture: F = W Blood and muscle pH: F = W Astaxanthin content: F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 1+	Fat content: F > W	Age	(Wolters et al., 2009)
	Freshwater, 0+ (liver)	Liver lipid content: F ≠ W Muscle lipid content: F = W	Size, Age	(Neregard et al., 2008)
Swimming and cardiac performance	Freshwater, adult 3+	Swimming performance: F = W Cardiac output, heart rate and stroke volume: F = W	Age	(Dunmall & Schreer, 2003)
	Freshwater, 0+	Swimming performance: F > W Respiratory training response: F < W	Size	(Zhang et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 8 Common-garden comparisons of disease susceptibility of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Salmon lice (*Lepeophtheirus salmonis*, Crustacea)	Salt water, 4 months post-transfer	Infection levels: F ≥ W	Age	(Glover et al., 2004)
	Salt water, 1–8 months post-transfer	Infection levels: F > H = W	Age	(Glover & Skaala, 2006)
Furunculosis	Freshwater, 1+	Mortality: F = H = W (after controlling for body size)	Age	(Glover, Bergh et al., 2006)
ISAV	Freshwater, 1+	Timing of mortality and overall mortality: F = H = W	Age	(Glover, Skar et al., 2006)
Vibriosis	Freshwater, 1+	Mortality: F ≤ W	Age	(Lawlor et al., 2009)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

present in very low frequencies in the population, which are rapidly lost within just a few generations due to founder effects or genetic drift. Due to founder effects, finite population size and more or less complete genetic isolation (except where strains have been mixed), reductions of up to 50% in allelic variation in highly polymorphic markers such as microsatellites have been reported in farmed strains as a consequence of genetic drift (Norris et al., 1999; Skaala et al., 2004). However, studies based on bi-allelic markers or markers with few alleles have not observed such strong reductions in genetic variation (Makinen, Vasemagi, McGinnity, Cross, & Primmer, 2015; Skaala et al., 2005; Vasemagi et al., 2012). In fact, Vasemagi et al. (2012), observed non-significant differences in the levels of diversity between wild and domesticated strains, and one comparison showed higher diversity in the domesticated strain compared to its wild progenitor. The disproportionate loss of alleles in highly polymorphic as opposed to bi-allelic makers such as SNPs is expected and has been well documented in other organisms taken into culture, and even under strong inbreeding regimes (Hamre, Glover, & Nilsen, 2009; Skern-Mauritzen et al., 2013).

The effect of marker type on levels of genetic diversity within and among farmed strains and wild populations is further evidenced in studies of mtDNA. Analysis of mtDNA haplotypes in four Norwegian farmed strains and four Norwegian wild populations has revealed greater numbers of haplotypes in the farmed strains, even when the same strains simultaneously displayed reduced diversity in highly polymorphic markers (Karlsson et al., 2010). This result is counterintuitive given that the effective population size for mtDNA is normally lower than for nuclear loci, reflecting haploid and maternal inheritance of mtDNA. However, there are two possible explanations. First, farmed strains were founded using multiple geographically diverse wild populations (Gjedrem, Gjoen et al., 1991) and consequently were established with a larger number of mtDNA haplotypes than would be found in any typical wild population. Second, the breeding schemes often employed in aquaculture involve using more females than males

TABLE 9 Common-garden comparisons of farmed and wild salmon under seminatural conditions

Trait	Study area	Life stage	Feed	Primary observations	Reference
Reproduction	Circular stream channels	Parr	Natural	Spawning success: F > H = W Fertilization success: F=H ≥ W	(Garant et al., 2003)
		Parr	Natural	Aggression: F = H = W. Onset of spawning: F = W < H (late spawning in H) Fertilization success: H > W > F	(Weir et al., 2005)
Growth, survival and maturation	Circular stream channels	Parr	Natural	Growth rate: F < W (size matched prior to experiment). Predation-related growth depression: F < W (n.s. trend). Natural mortality/recovery rate: F = W	(Fleming & Einum, 1997)
		Parr	Pellets (restricted)	Growth: F > H > W (less differences than under hatchery conditions). Mortality: F = H < W	(Solberg, Zhang et al., 2013)
		Parr	Pellets (restricted)	Susceptibility to an artificial predator: F = H = W	(Solberg et al., 2015)
		Parr	Natural	Mortality and dispersal: F = W	(Sundt-Hansen et al., 2015)
		Parr	Pellets	Growth rate: F > H > W Density effect on growth: F = H = W	(Harvey, Juleff et al., 2016)
	Oblong stream channels	Parr	Natural	Mortality: F < W, high density = low density. Body mass: F > W, high density < low density	(Sundt-Hansen et al., 2015)
	Tanks with gravel	Parr	Live feed + pellets	Growth: F > W Size selective predation susceptibility: F < W Predation-related stress tolerance: F > W Parr maturation: F < W	(Debes & Hutchings, 2014)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

as broodstock. In turn, this provides a higher effective population size for maternally inherited mtDNA that would be expected at more equal sex ratios.

Large-scale genomewide SNP panels have been used to investigate genetic differences within and among farmed and wild salmon strains and populations. SNP panels, in addition to partial or whole-genome resequencing approaches, offer at least two main advantages over other marker types in characterizing genetic differences between farmed strains and wild populations. Firstly, the number of genetic markers available for routine screening, ranging from 100s to 100 000s of markers, increases the likelihood of finding a diagnostic subset that distinguishes routinely between farmed strains and wild populations. Karlsson et al. (2011) screened 12 farmed strains and 13 wild populations for a 7K SNP chip and identified a set of 60 SNPs that were collectively diagnostic in distinguishing between wild Norwegian populations and Norwegian farmed strains. They concluded that these SNPs potentially reflect signatures of selection based on (i) common shifts in allele frequencies in the farmed strains away from those of the wild populations and (ii) overall higher levels of genetic differentiation among different farmed strains than among the different wild populations, consistent with information on the origin of the farmed stains.

The second advantage of high-density genomewide SNP panels and sequencing approaches is the ability to identify genomic regions under selection and associated with the domestication process, by finding SNPs that map to traits, or are linked to loci influencing traits that are the targets of selection in aquaculture. Two studies have conducted genome scans for signatures of selection on the same samples among three independent domesticated/captive salmon strains and their wild progenitors using 331 (SNPs and microsatellites) markers and a 15K SNP chip (~4K polymorphic SNPs after filtering and quality control), respectively (Makinen et al., 2015; Vasemagi et al., 2012). These studies identified few genomic regions/outliers under selection, and the regions identified were not always the same in the different comparisons.

These authors, as well as an earlier study (Karlsson & Moen, 2010), demonstrated that the power to detect selection at a single locus depends primarily on the number of generations since domestication, the strength of selection and the number of populations under investigation. It should also be noted that in these two studies (Makinen et al., 2015; Vasemagi et al., 2012), both farmed and hatchery strains were used. The hatchery strains were based on captive-bred populations, which were not subject to artificial selection and were deliberately released into the wild as smolts for supplementation and experimental purposes and therefore the type and strength of selection these fish were subjected to will differ considerably from that which farm strains are exposed to. This may go some way to explaining the observations reported (Makinen et al., 2015; Vasemagi et al., 2012). Alternatively, and importantly, many traits subject to selection are complex, that is, with several different loci underlying the traits and with epistatic effects. This may leave weak footprints on each of the loci involved, even though the phenotypic effects are strong (McKay & Latta, 2002; Pritchard & Di Rienzo, 2010). Genome scans therefore have limitations in identifying genomic footprints of the selection that has occurred in aquaculture, but use of novel statistical methods has provided promising results (Brieuc, Ono, Drinan, & Naish, 2015).

A recent study comparing the Cermaq strain (which is a strain reared in British Columbia, Canada, estimated to have undergone 12 generations of selection) with four wild Norwegian populations using the 7k SNP chip identified 44 loci under selection (Gutierrez, Yanez, & Davidson, 2016). Many of these loci were associated with molecular functions that could be related to selection for economically important traits such as growth, as well as traits that would be likely connected with the process of domestication, such as the response to pathogens and environmental stressors. With an increasing number of SNPs available for screening, higher density maps are expected to lead to a higher probability of identifying genomic regions under selection (Davey et al., 2011) and should be investigated on a wide range of farmed strains which should vary in their origin and length of time they have been domesticated.

3.3.2 | Studies of gene transcription

A handful of studies have investigated gene-transcription profiles of farmed and wild salmon reared under controlled conditions. These have revealed a large number of different expression profiles during very early developmental stages (Bicskei et al., 2014; Bicskei, Taggart, Glover, & Bron, 2016; Roberge, Einum, Guderley, & Bernatchez, 2006; Roberge, Normandeau, Einum, Guderley, & Bernatchez, 2008), as well as later juvenile and post-smoltification stages (Debes, Normandeau, Fraser, Bernatchez, & Hutchings, 2012; Normandeau et al., 2009) (Table 2).

A recent study conducted on hatchery-raised steelhead trout demonstrated that just a single generation of domestication can cause changes in gene-transcription profiles (Christie, Marine, Fox, French, & Blouin, 2016). However, gene transcription is strongly influenced by environmental variation (e.g. Evans, Hori, Rise, & Fleming, 2015), which makes extracting general trends in transcription patterns between farmed and wild fish, among the various studies conducted (which includes life stage and environmental variation), a challenge. This is further complicated by the fact that gene-by-environment effects play a significant role in the transcriptomic responses of farmed salmon (Evans et al., 2015) and that transcription profiles for genes that are differentially expressed between the farmed and wild salmon do not always display additive genetic variation, and thus, hybrids often display non-intermediate profiles (Bicskei et al., 2016; Normandeau et al., 2009; Roberge et al., 2008). These complexities make our prediction of the consequences of different gene expression in farmed salmon and their offspring in the wild difficult.

Despite the highlighted challenges, studies of gene transcription in salmon have revealed some trends and identified processes that may be linked with domestication-mediated evolutionary changes. Processes such as environmental information processing and signalling pathways in addition to immune-related genes have been reported to be more highly expressed in wild relative to farmed salmon (Bicskei et al., 2014, 2016). In contrast, processes

linked to, for example, protein synthesis and metabolism have been demonstrated to be upregulated in farmed compared to wild salmon (Bicskei et al., 2014; Roberge et al., 2006). The latter is also supported from evidence in other salmonid species exposed to domestication regimes (Devlin, Sakhrani, Tymchuk, Rise, & Goh, 2009; White et al., 2013). While the degree to which the changes in these processes reflect evolutionary responses in response to directional and domestication selection remains unquantified, indirect selection for a more docile animal that displays higher growth rates is consistent with some of the apparent transcription trade-offs revealed by these studies. Furthermore, gene-transcription studies in coho salmon (*Oncorhynchus kisutch*, Salmonidae) (Devlin et al., 2009) and rainbow trout (Devlin, Sakhrani, White, & Overturf, 2013) have revealed that domestication changes seem to stimulate similar molecular pathways as growth hormone (GH) treatment. This is also possibly the case in salmon, a suggestion indirectly supported by the fact that GH treatment gives a stronger growth response in wild as opposed to domesticated salmon, suggesting overlapping pathways already partially stimulated or utilized through domestication (Neregard et al., 2008).

Investigations among multiple salmon strains and backcross variants have led to the conclusion that many of the differences in gene-transcription patterns between farmed and wild salmon may be population specific (Normandeau et al., 2009). However, other studies have found evidence of parallel changes in different domesticated and wild strains (Roberge et al., 2006), which further supports the notion that many of the observed transcriptional differences between farmed and wild salmon are linked to domestication. The magnitude of differences in gene-transcription profiles between farmed and wild salmon has also been reported to increase with age of the fish. For example, in an experiment investigating transcription in yolk-sac fry and after first-feeding fry, a greater number of differences in transcription patterns were observed between the farmed and wild groups at the first-feeding stage (Bicskei et al., 2014). These changes between pre- and post-external feeding stages included differential upregulation of metabolic-linked processes in the farmed fry, which could be linked (causatively or otherwise) with their genetically determined higher growth rates.

3.3.3 | Comparative studies under hatchery or seminatural conditions

Here, we review papers comparing farmed and wild salmon that have been reared under identical conditions from hatching (with a few exceptions in time due to some of the above-mentioned limitations with comparative studies of fast-growing farmed versus wild salmon) (Table 3–9). Thus, the experiments can be regarded as "common garden" where the observed phenotypes of farmed and wild salmon are the result of the expression of their genotypes under those specific sets of conditions (de Villemereuil, Gaggiotti, Mouterde, & Till-Bottraud, 2016). Experiments where the salmon were raised in different environments (i.e. hatchery vs. wild or in different hatcheries) have not been included as any potential differences reflect both environmental and genetic differences. Using the common-garden approach, experimental studies under hatchery or net pen conditions have revealed genetic differences between farmed and wild salmon in traits ranging from growth (Table 3) to maturation and developmental timing (Table 4), behavioural traits (Table 5), plasticity (Table 6), morphology and physiology (Table 7) and disease tolerance (Table 8). A few comparative studies, focusing on traits such as survival and growth, parr maturation, and predation, have also been performed under seminatural conditions (Table 9). These studies have primarily involved juveniles, possibly due to logistical and experimental constraints; however, some studies have been conducted for the entire life cycle.

The trait displaying the largest and most consistent difference between wild and farmed salmon is growth (Table 3). Selection for increased growth rate has been the backbone of the domestication breeding programmes from the initiation of the industry (Gjedrem, 2000, 2010), and it is therefore expected that this is the trait displaying the greatest divergence. While growth rate and fish size have been measured in slightly different ways between studies, it is estimated that a ~10%–20% gain in growth rate has been obtained per generation from the early stages of domestication (up to the 5th generation) due to selection (O'Flynn, Bailey, & Friars, 1999; Thodesen et al., 1999).

The results of more recent studies, performed on farmed salmon of 7–10th generation vs. wild salmon, have reported continuously increasing ratios in body size between farmed fish and wild fish when reared under common-garden rearing conditions (Glover et al., 2009; Solberg, Glover et al., 2013; Solberg, Zhang et al., 2013), illustrating that a quantifiable genetic gain per generation is still being achieved (Figure 4). For example, size ratios of approximately 2–2.5:1 were observed for both juveniles and adults in a study conducted with approximately 7–8th generation of Norwegian farmed salmon (Glover, Ottera et al., 2009), while a more recent study using juveniles of the same farmed strain in the approximately 9–10th generation displayed a ratio of approximately 2.9:1 under standard hatchery conditions and 3.5:1 under hatchery conditions where growth was restricted through chronic stress (Solberg, Glover et al., 2013).

In Canadian salmon, growth ratios of approximately 3:1 have been documented between juvenile farmed salmon exposed to five generations of selection in respect of their wild founding population (Debes & Hutchings, 2014). Although growth ratios as high as 4.9:1 have been documented between farmed and wild salmon (Solberg, Zhang et al., 2013), it is worth pointing out that not all studies with domesticated salmon of ~10 generations have revealed such high size ratios under hatchery conditions (Harvey, Glover et al., 2016; Solberg et al., 2016) (Figure 4). The underlying causes of variations among studies remain unclear, although population-specific factors contribute.

Most of the growth studies have compared a single farmed strain with a wild population, and growth has always been higher in the farmed fish under hatchery conditions. Furthermore, when F1 hybrids have been studied, they have always displayed intermediate or close to intermediate growth rates (Glover, Bergh, Rudra, & Skaala, 2006; Glover, Ottera et al., 2009; Solberg, Glover et al.,

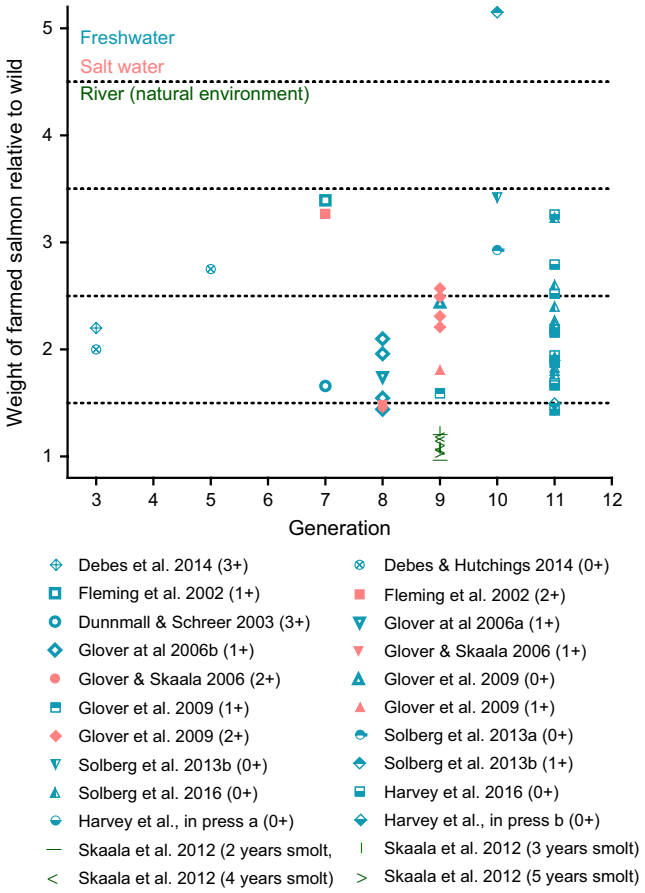

FIGURE 4 Growth of farmed relative to wild salmon. Open symbols (blue) illustrate studies performed in freshwater in tanks; closed symbols (coral) illustrate studies performed in salt water in tanks or sea cages; line-based (- | > <) symbols (green) illustrate studies performed in a river under natural conditions. The two studies performed on Canadian farmed salmon are illustrated with open symbols with a cross; all other studies are performed on Norwegian farmed salmon. Only common-garden studies documenting growth, in terms of body weight (i.e. not length), in non-sized matched salmon of similar age, sampled after their first summer are included. Not all studies report the exact number of generations of domestication; thus, ± one generation may occur. Growth differences under experimental treatments, that is differing temperature, salinity, feed levels, are not included here. Only studies performed under standard fish farming or natural conditions are included, one exception is Debes & Hutchings, 2014 that is performed under seminatural conditions

2013; Solberg, Zhang et al., 2013) which is consistent with the concept that the majority of the variation for this trait is under additive genetic control of many genes. However, non-additive variation for growth has been observed and may account for as much as 25%–50% of the expression of this trait, as has been documented in multigenerational hybrids and backcrossed variations between these forms (Debes, Fraser, Yates, & Hutchings, 2014). Thus, non-additive genetic factors, such as dominance, overdominance and epistasis, may make it hard to predict the outcome of introgression between farmed and wild salmon, especially as non-additive inheritance of other traits of importance for survival in the wild has also been documented (Einum & Fleming, 1997; Houde, Fraser, & Hutchings, 2010a).

Higher heritability estimates for growth have been documented in wild relative to farmed salmon (Solberg, Glover et al., 2013). As a larger portion of the phenotypic variation of this trait is thus attributable to genetic variation in the wild as compared to the farmed salmon, this finding indicates a slightly reduced genetic variation for growth in farmed salmon. Such a finding is consistent with the general predictions of domestication and furthermore supported by the detection of reduced variation for both mass and length in farmed, as compared to wild salmon (although not significantly different) (Morris et al., 2011).

After growth, behaviour represents one of the major areas where the genetic differences between wild and farmed salmon have been investigated. Behavioural studies can be broadly grouped into those investigating aggression and competition and those addressing predator avoidance. Both sets of traits are highly important in salmonids in the natural environment, enabling individuals to be able to compete for resources such as territories and food, while avoiding predation. Behavioural changes linked directly or indirectly with the process of domestication have been well studied in fish (Huntingford, 2004; Ruzzante, 1994). Examples of both increases and decreases in aggression have been documented, and it has been suggested that the direction of the behavioural response is likely to be specific to the conditions in which the domestication selection was imposed, and therefore, which behaviour (e.g. increased or decreased aggression) favours access to and use of resources under the context-specific conditions (Ruzzante, 1994). Thus, it is perhaps not surprising that, when one looks specifically at comparative studies in farmed and wild salmon, examples of farmed salmon showing increased (Einum & Fleming, 1997; Houde et al., 2010a), similar (Fleming & Einum, 1997; Houde et al., 2010a) and decreased (Fleming & Einum, 1997) aggression and dominance abilities as compared to wild fish have been observed. Hybrids have been shown to display both intermediate competitive levels and to dominate both their farmed and wild counterparts (Einum & Fleming, 1997; Houde et al., 2010a). However, prior residency (Metcalfe, Valdimarsson, & Morgan, 2003), and possibly fish size (Symons, 1968), remains as important factors influencing such behavioural trials and given the large growth differences between the groups this makes such experiments challenging and potentially difficult to interpret, also when size-matched individuals have been used.

Predation–avoidance behaviour experiments have revealed genetic differences between farmed and wild salmon. Although experiment designs have varied, the few studies published have demonstrated that farmed fish display more naive behaviour towards artificial predators such as shorter times to re-emergence following exposure to an artificial predator (Einum & Fleming, 1997; Fleming & Einum, 1997; Houde, Fraser, & Hutchings, 2010b). This behaviour has most likely arisen due to the relaxation of natural selection in the hatchery environment, combined with a positive selection for growth and thus tolerance to the hatchery conditions where predators do not reflect a selective force. Indeed, such a trade-off between growth and survival

rates has been documented in other salmonids (Biro, Abrahams, Post, & Parkinson, 2004, 2006).

Further evidence of reduced predator awareness comes from studies which demonstrate that offspring of wild salmon displayed a drop in growth in the presence of a predator (with low or no predation), while in contrast, domesticated salmon show a smaller decline in growth (Fleming & Einum, 1997) or no decline at all (Debes & Hutchings, 2014). Given the fact that the offspring of farmed salmon display a lower survival than that of wild salmon in the wild (see section below) and that predation is a known component of mortality of salmonids in freshwater (Feltham & MacLean, 1996; Henderson & Letcher, 2003; Vik, Borgstrom, & Skaala, 2001), it is likely that behavioural traits have changed as a result of domestication and therefore contribute to the lower fitness of the progeny of farmed fish in the wild. Nevertheless, the direct connection between increased risk taking behaviour- and predation-related mortality rates in farmed as compared to wild salmon is yet to be demonstrated (Skaala, Glover, Barlaup, & Borgstrom, 2014; Solberg, Zhang, & Glover, 2015).

3.3.4 | Studies conducted in the natural environment

Common-garden experiments undertaken in the wild are a relatively recent development and only made possible with the development of DNA profiling for accurate parentage assignment (Ferguson et al., 1995). Previously, salmon had to be reared separately before they were large enough to tag physically. By taking experiments into the wild, experimental populations can be exposed to the vicissitudes of complex ecosystems, which are impossible to replicate in the laboratory. These involve both the river and the sea, and the transition between them.

Depending on the life-history stage investigated, studies conducted in the wild also display a huge range in spatial scale, from tens of metres to thousands of kilometres. A range of environmental factors vary continuously in the wild, for example temperature, light, water velocity, pH and salinity. In turn, these factors pose local biological challenges in respect of food availability, exposure to pathogens, parasites and predators, and interspecific competition for resources. Typically for wild salmon, more than 90% of the eggs introduced into the river will be dead by the end of the first summer, roughly only 1 or 2% of eggs will make it to the smolt stage and usually no more than 10% and often less of the smolts that go to sea will make it back from the ocean to spawn. Assuming that the traits contributing to fitness are heritable and there is sufficient variance in survival among families within different groups, such high rates of attrition provide the opportunity for intense levels of natural selection. Any mismatch between the fish and the environment will be readily exposed, revealing adaptive differences between native and non-native populations. Thus far, only three published studies have addressed survival and development of farmed, hybrid and wild salmon in the natural environment. This is not surprising given the fact that they are exceptionally demanding on research facilities, in addition to experimental and financial logistics.

The first common-garden study in the wild was conducted in Ireland and involved planting eggs of Norwegian farmed (Mowi strain), F1 hybrid and wild (local) parentage into a section of the Burrishoole River (McGinnity et al., 1997, 2003; Reed et al., 2015). The progeny of the experimental parental fish was sampled in the river at different life-history stages using a combination of electrofishing, together with downstream (juvenile seaward migration) and upstream (adults returning to spawn) traps, and was identified to family and experimental group using DNA profiling. As insufficient adult returns would have been obtained from smolts produced naturally in the river, the marine phase of the life cycle was examined by ranching, that is smolts from the same families that were introduced into the experimental river were reared in a hatchery and released to the sea to complete their life cycle and captured and sampled on their return. These fish were followed through two generations using the surviving adults returning from the sea to propagate the second generation. The authors concluded that the lifetime survival of farmed fish was just 2% of wild fish and that the relative fitness increased along a gradient towards the offspring of a F1 hybrid survivor spawning together with a wild salmon (=wild backcross) which displayed a lifetime survival of 89% compared to the offspring of two wild salmon, indicating additive genetic variation for survival (McGinnity et al., 2003). This was a fundamental observation.

The study dispelled the previously held idea that farm-wild hybrids might display enhanced performance due to heterosis (hybrid vigour). Secondly, it showed that there was likely to be a penalty in respect of fitness following hybridization and introgression of farmed escapees into recipient wild populations. This is extremely important as in many cases where escaped farmed salmon enter a river, production of F1 hybrids rather than pure farmed offspring is the outcome (in part due to the differences in spawning success between female and male farmed escapees). Thus, part of the potential wild juvenile recruitment is converted to hybrids in the first generation, and to backcrosses in the second, and subsequent generations (Figure 3). The lower lifetime reproductive success of hybrids will, therefore, reduce the average fitness of the wild population. It also suggested the possibility of a predictive capability, which would have general applicability with respect to establishing the likely biological consequences for affected populations where escaped salmon may have spawned in the wild. Additive genetic effects were also apparent for most of the phenotypic traits measured in the Burrishoole experiment related to growth and performance with mid-range values found for juvenile size at age, including 0+ and 1+ parr; smolt size; propensity for precocious maturation; tendency for autumn smolt migration; sea age of maturity (McGinnity et al., 1997, 2003, 2007; Reed et al., 2015); these intermediate phenotypes being neither adapted to the river nor the farm. The authors thus further concluded that repeated invasions of farmed salmon in a wild population will cause the fitness of the recipient native population to seriously decline and potentially in extreme cases enter an “extinction-vortex” should the incidence of escapes in terms of numbers and frequency be sufficiently large and recurring.

The extension of the Burrishoole experiment into the second generation also facilitated a rare insight into the operation of outbreeding depression in the F2 generation (McGinnity et al., 2003). The highest egg mortality occurred in the F2 hybrid group and most

probably reflected outbreeding depression as might be expected from a breakdown of co-adapted sets of alleles following recombination of parental chromosomes, that is principally the "intrinsic" interaction between genes (Edmands, 2007). Remarkably, the F2 hybrids performed extraordinarily well subsequently and were anomalously, very highly represented in the river as 0+ and 1+ parr relative to the other groups. In the case of certain F2 hybrid families, a plausible explanation could be that the blend of divergent wild and farmed parental genomes produced rare offspring recombinant genotypes that were fortuitously well adapted to the local conditions through heterosis (Reed et al., 2015).

The Burrishoole study also yielded some valuable ecological insights into the interaction of farmed and wild origin fish. While the farmed and hybrid offspring of farmed parents showed reduced survival compared to wild salmon, they grew faster as juveniles and appeared to displace slower growing and thus smaller wild parr. Where suitable habitat for these displaced parr is absent, this competition would result in reduced wild smolt production. The effects of this competitive displacement were more profound at higher stocking densities (eggs planted at a density of 5.8 m^{-2} in 1993 versus eggs planted at a density of 8.4 m^{-2} in 1994).

It was apparent from the relative survival of the progeny of farmed and wild fish in the Burrishoole experiment that the marine environment presented the greatest challenge to the non-native fish; an approximate twofold reduction in survival for farmed fish in the river, when planted as eggs, was more than ten times lower in the sea, when released as smolts. It would appear that the traits associated with the marine environment or the transition between local river environments and marine environments (or indeed carry-over effects from the freshwater environment that are important for life in the sea) are of substantially greater importance in respect of local adaptation than the more obviously local factors in the river environment. Such traits may include ocean entry timing, predator avoidance and the ability to orientate into favourable ocean currents for transportation to feeding grounds. Likewise, a successful return to the natal river and arrival to the spawning grounds will be contingent on homing orientation; time spent at sea, timing of return and timing of river entry.

The seeming discordance between the farmed phenotype and the marine environment regarding Irish conditions would prove a serious impediment to subsequent gene flow to the wild from this source and to the integrity of the wild population. Compared to the pure farmed progeny, the relative success of the various combinations of hybrids was much greater and would indicate these as a more likely conduit for the transfer of genetic material from farmed fish into the wild. These studies remain as the only two-generation comparison of farmed and wild salmon in the natural environment.

In Norway, a slightly different but complimentary experiment to the study conducted in Burrishoole was conducted in the River Imsa during the same time period (Fleming et al., 2000). Here, the authors released adult salmon of farmed (the Norwegian AquaGen strain) and wild (local) origin above a two-way fish trap in the River Imsa, once they had been biopsy sampled. Thus, this study incorporated an important additional behavioural component in respect of reproductive performance of farmed and wild salmon into the experimental design. Therefore, the fish were allowed to spawn naturally in the river and their offspring were sampled by electrofishing, in addition to downstream and upstream traps located in the river. This study reported a breeding success of farmed salmon at less than one-third the breeding success of wild salmon and a lifetime fitness of farmed salmon from one generation to the next (i.e. escaped adult fish in the river to adults returning from the sea) of 16% in comparison with wild salmon (Fleming et al., 2000).

The observed difference in survival between farmed and wild salmon was very similar in magnitude to the differences observed in Burrishoole in Ireland. It is also notable that the rank order of wild > hybrids > farmed (for survival) was also found to be the same. Important additional data from this study were the fact that population productivity, measured by the total number of smolts produced, and the numbers of smolts of wild parentage, dropped by c. 30% following the permitted spawning intrusion of farmed salmon. The observed reduction in total and wild smolt productivity was attributed to the fact that the offspring of the farmed and hybrid salmon competed with wild salmon for both territory and resources, and the dynamics of this may vary across life-history stages (Sundt-Hansen, Huisman, Skoglund, & Hindar, 2015). The study also indicated significantly higher juvenile and smolt size for fish with farmed parents compared to the fish of wild parents and a significantly lower age at smoltification (see Figure 2 in the paper).

As noted earlier, observations on the reproductive behaviour of farmed and wild salmon by Fleming et al. (2000) showed that adult farmed fish were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fish. Moreover, this inferiority was sex-biased, being more pronounced in males than females, identifying it as an important route for gene flow involving native males mating with farmed females. This confirms the earlier behavioural studies conducted in seminatural spawning arenas (Fleming et al., 1996). The lower early survival of the juvenile farmed genotypes in the Imsa River experiment (Fleming et al., 2000) also appeared to constrain invasion by farmed escapes, but it did so to a lesser extent than breeding. As was reported in the study conducted in Burrishoole (McGinnity et al., 1997), results from the Imsa experiment detected indications of a competitive effect with displacement of the progeny of wild fish with offspring distributions differing despite native and farmed females having had similar spawning locations.

In contrast to the Burrishoole study, no differences in marine survival and age of maturity were found between the progeny of wild and farmed salmon in the Imsa experiment. This illustrates the contribution of life-history variation to fitness in given circumstances, as the parental fish differed markedly between both experiments in respect to their phenotype, size and age of maturity. At Imsa, the farmed salmon parents used in the experiment were 1sea winter (SW) and 2SW fish and were relatively well matched in size to the wild fish. In contrast, large 3SW and 4SW fish of Norwegian farmed origin were used in the initial 1993 and 1994 Irish experiments, while 2SW fish of the same provenance were used in the 1998 experiment, as compared to the small 1SW Burrishoole wild population.

The most recent published study to address the relative fitness of farmed and wild salmon in a natural environment was conducted in the River Guddal in Norway (Skaala et al., 2012). These authors used a similar design to the Irish study, planting nearly a quarter of a million eggs of farmed (a mixture of Norwegian farmed fish with unknown background, and Norwegian Mowi), hybrid and wild (non-local, Lærdal from the Norwegian gene bank) parentage into the river, and followed their growth and survival until smoltification. The study included planting out three cohorts in successive years with gradually increasing egg density and therefore the level of competition, and permitted for the first time, comparisons of family as well as group performance (farmed, hybrid and wild). It showed several important results.

Large differences in survival were observed among the 69 experimental families from egg-smolt, both within and among experimental groups. Interestingly, the highest surviving family was of farmed parentage in the first cohort, although wild, hybrid and farmed families were among the highest and lowest ranked families for survival. Farmed salmon smolts were also on average larger than the wild smolts in the Guddal study (7%, 25% and 6% larger in cohorts one, two and three, respectively). The authors also detected a significant positive effect of egg size on survival, a phenomenon noted in other studies of salmonid early life history in the wild (Einum & Fleming, 2000). In the Guddal study, farmed salmon eggs were larger than the wild salmon eggs (this will vary from case to case), and when this effect was controlled for in the statistical model applied, the offspring of farmed fish displayed a significantly higher mortality than the offspring of wild fish (relative farmed family survival = 0.8 and 0.62 of wild fish for cohort two and three, respectively). Thus, the relative survival of the farmed fish decreased with an increase in density and competition across the cohorts planted. When looking at half-siblings where egg size was identical, families sired with wild males displayed higher survival than families sired with farmed males in 15 of 17 pairwise comparisons. A subsequent analysis by Reed et al. (2015) on the Burrishoole data also showed substantial interfamily differences in survival and size at age in 0+ and 1+ parr. They found egg size had a significant positive effect on the fork length and mass of 0+ fry caught by electrofishing, whereas no egg size effect was found for 1+ parr sampled the following year. However, positive effects of egg size on survival of both 0+ and 1+ parr were also found. The Guddal study also revealed that farmed and wild salmon overlapped in diet in the river, an observation also reported from an earlier small-scale planting study (Einum & Fleming, 1997) and from the full-generation study in Imsa (Fleming et al., 2000).

Studies validating and examining the underlying details, mechanisms and genomics of the observed survival differences between offspring of farmed and wild salmon in natural habitats have also been published using data from the study in Burrishoole and Guddal (Besnier et al., 2015; Reed et al., 2015). These studies have revealed further details, including identification of QTLs for growth and importantly survival (Besnier et al., 2015), and provided estimates for heritability in the wild (Reed et al., 2015). In the case of salmonid fish, quantitative-genetic parameters, such as estimates of heritability, calculated under farm or hatchery conditions have limited relevance for wild populations given the environmental sensitivity of these parameters. This further justifies the need to undertake common-garden experiments under natural conditions.

To address the ecological mechanisms underlying the observed differences in survival between the offspring of farmed, hybrid and wild salmon in the wild, an additional experiment was conducted in the River Guddal (Skaala et al., 2014). Extensive electrofishing was conducted for wild brown trout (*Salmo trutta*, Salmonidae) in the proximity where the experimental eggs were planted out. Of the 760 trout non-lethally sampled, 4.2% of them had ingested a total of 46 salmon fry. These fry were thereafter genotyped to identify them to experimental family and farmed, hybrid or wild group. When predation of these groups was compared to the numbers of eggs released for each group, there was no significant difference in predation between the farmed, hybrid and wild offspring. A similar result has also been reported in seminatural arenas (Solberg et al., 2015). These observations stand in contrast to the results of predator awareness or avoidance studies where domesticated salmon have been demonstrated to display less caution than wild salmon (Einum & Fleming, 1997; Fleming & Einum, 1997; Houde et al., 2010b).

Despite the obvious differences in provenance, history of domestication in farmed strains and environmental context of the experiments reported in the studies above, there is a remarkable consistency in the outcomes of the experiments in Norway and Ireland and among cohorts compared in the same locations (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012). Furthermore, the recurring evidence of additive genetic effects contributes to explain observed traits and rates of survival. While all experiments by their nature will be somewhat case or situation specific, not unexpectedly there are also some dissimilarities between experiments, particularly in the magnitude of the differences. However, the basic similarities in outcomes suggest that results have general transferability in considering biological consequences to actual escape events.

4 | DISCUSSION OF FITNESS IMPLICATIONS FOR WILD POPULATIONS

4.1 | Will there be changes in juvenile and adult abundance?

Density-dependent factors set the limit on a river's carrying capacity for juvenile and smolt production (Bacon et al., 2015; Jonsson, Jonsson, & Hansen, 1998). Offspring of farmed salmon compete with wild salmon for resources such as food and space (Einum & Fleming, 1997; Fleming et al., 2000; Skaala et al., 2012). Therefore, when farmed salmon manage to spawn in the wild, and their offspring (either from two farmed parents or from more likely a farmed and a wild parent) constitute a component of a given river′s juvenile population, the production of juveniles with a pure wild background (i.e. two wild parents) will be depressed through competition for these resources.

Theoretical studies suggest that populations that are well adapted to their local environments increase towards the carrying capacity, while those whose trait values lie far from the local optimum decline (Burger & Lynch, 1995; Garcia de Leaniz et al., 2007; Kirkpatrick &

Barton, 1997). In addition, a demographic penalty is expected when populations undergo the process of adapting to changing environments (Burger & Lynch, 1995; Kirkpatrick & Barton, 1997). This type of demographic penalty might be assumed to occur in native populations following spawning intrusion of mal-adapted farmed escapees. In this case, the population rather than the environment changes, although both plausibly could occur at the same time. Field studies of salmon agree with these theoretical predictions and indicate that the total production of smolts in a river (i.e. fish of all genetic backgrounds) may decrease following spawning intrusion of farmed salmon (Fleming et al., 2000; McGinnity et al., 1997). While the mechanisms underpinning the decrease are not completely understood, this may arise because farmed salmon offspring and hybrids can competitively displace wild salmon under certain environmental conditions (McGinnity et al., 1997; Sundt-Hansen et al., 2015), whereas their egg-to-smolt survival is lower than for wild offspring.

The effect on total productivity will also depend in part on whether selection against maladaptive farmed or introgressed salmon dominates before or after density-dependent selection has occurred and "thinned out" the total population (Baskett et al., 2013). If density-dependent selection occurs before selection against maladapted domesticated genotypes, there will be a drop in total numbers of smolts produced; however, if selection against maladapted genotypes occurs before or in concert with density-dependent selection, a drop in juvenile production is not necessarily expected. The competitive balance and impact on total smolt productivity may also be influenced by the level of farm-wild hybridization within a population (Houde et al., 2010a), and the density of the recipient population and level of juvenile competition (Skaala et al., 2012). Maternal factors, such as egg size variation, may also negatively impact total smolt production where farmed salmon eggs are larger than wild salmon eggs (Lush et al., 2014; Srivastava & Brown, 1991)), which may offer an initial maternal survival advantage (Skaala et al., 2012).

Introgression of farmed salmon may also decrease the number of fish returning to spawn in the wild beyond the potential reduction resulting from the reduced smolt migration alone. This is less well understood than freshwater effects. Studies of released smolts in the Burrishoole River in Ireland (McGinnity et al., 1997, 2003) found during the marine phase of the life cycle a lower survival of farmed and hybrid salmon offspring than those of wild salmon. No difference in marine mortality was observed between naturally produced smolts of farmed and wild salmon origin in the Imsa study, but later experiments based on smolt releases showed relative marine survival rates of farmed smolts to be 37% of wild smolts, with hybrid smolts not being significantly different to wild (Hindar et al., 2006). A decrease in marine survival would be expected to decrease adult returns in proportion to the extent that emigrating smolts are composed of farmed or mix farmed-wild individuals. This suggestion is supported by modelling (Baskett et al., 2013; Castellani et al., 2015). However, models have also indicated that changes (i.e. decrease) in the numbers of returning adults in admixed populations may be difficult to detect in non-experimental populations in the short-term. This is because the high natural variation in numbers of adult salmon returning to rivers due to variations in oceanic conditions (Friedland, Hansen, Dunkley, & MacLean, 2000; Jonsson, Jonsson, & Albretsen, 2016; Vollestad et al., 2009; Youngson, MacLean, & Fryer, 2002) may potentially mask short-term changes.

In general, the survival of salmon smolts on a trajectory of spending 3 years at sea as opposed to just one or two years is reduced (Chaput, 2012). It is therefore unknown to what degree the observed relative marine survival difference between farmed and wild salmon (McGinnity et al., 1997, 2003) is linked to inherent differences in survival between salmon that display 1–3 years in the sea, or to domestication-driven differences between farmed and wild salmon in general. In the Burrishoole River in Ireland, the native population was predominantly of 1 sea winter and the farmed strain multisea winter (which could have contributed to the observed difference). Despite the increased fecundity of the larger returning hybrid and multisea winter farmed salmon, this was not enough to prevent a drop in egg deposition due to their higher rates of marine mortality associated with their genetic heritage (McGinnity et al., 2003). This suggests that both the number of returning adults and the overall number of eggs deposited may decrease with the introgression of farmed salmon. However, the marine survival of farmed, hybrid and wild salmon is poorly studied compared to the freshwater stage of the life cycle.

4.2 | Will there be changes in phenotypic and life-history characters?

Farmed salmon are genetically different to wild populations. In whole-river experiments (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012), heritable differences in freshwater growth and body shape, timing of smolt migration, age of smoltification, incidence of male parr maturation, sea age at maturity and growth in the marine environment have been observed between the offspring of farmed and wild salmon. Therefore, where farmed salmon have introgressed in natural populations, it is expected that recipient populations will display changes in phenotypic and life-history traits in the direction of the intruding farmed strains. Significantly, the phenotypes of the hybrid progeny of farmed and wild crosses have, in many of the experiments undertaken in the wild, been shown to be intermediate for the life-history traits listed above (McGinnity et al., 2003, 2007) and thus maladapted to both environments. Any changes in the direction of the farmed strain are likely to be associated with and contributing to a loss of fitness, given that phenotypic and life-history traits are strongly associated with fitness in the wild (Fraser et al., 2011; Garcia de Leaniz et al., 2007; Taylor, 1991).

The magnitude of genetic changes in phenotypic and life-history traits will scale with the level of introgression and most likely follow a dose–response relationship (Castellani et al., 2015). Changes caused by low or modest levels of genetic introgression may be difficult to detect, especially in the short term (Castellani et al., 2015), given that many phenotypic traits in salmon are highly plastic (Debes et al., 2014; Garcia de Leaniz et al., 2007), and yearly environmental variation, as well as environmental change through time, may also influence life-history traits. This has recently been observed for age of maturity in

wild salmon in relation to changing sea temperatures (Jonsson et al., 2016), which may serve as a confounding effect on genetic changes in this trait due to introgression. Other mechanisms, for example high mortality during early life-history stages and lower survival of farmed salmon juveniles (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012), may also collectively contribute to masking population-level changes in phenotype and life history.

A good example to illustrate the potential challenge(s) to identifying and quantifying genetic changes in fitness-related traits in wild populations as a consequence of introgression of farmed escaped salmon is growth. It is both one of the most plastic traits in fish (Debes et al., 2014; Karjalainen et al., 2016) and the one that displays the greatest genetic difference between wild and farmed salmon (Table 3). Farmed salmon typically achieve body weights 2–3 times greater than wild salmon when reared in common-garden studies under hatchery conditions. However, when investigated in the wild, freshwater growth differences between the offspring of farmed and wild salmon are much smaller than in the hatchery, sometimes by one or more orders of magnitude less (Fleming et al., 2000; Reed et al., 2015; Skaala et al., 2012) (Table 3; Figure 4). Given the reaction norm variation of this trait seen across divergent environmental conditions (Table 5), under low or perhaps even modest levels of genetic introgression and hybridization, changes in wild growth rate and body size in a population will be difficult to detect. More sensitive experimental approaches, for example, examining the genetic background and growth rates of individuals within a population, will be needed to assess whether changes have occurred. Despite these challenges, changes in some traits may be detectable where farmed populations show a large deviation from an impacted wild population. This is the case, for example, where adults in wild stocks return predominantly after 1 sea winter as is the case on the West Coast of Ireland, Scotland and in Newfoundland, as compared to farmed stocks where most are multisea winter, although there can be considerable variation from river to river.

In an investigation of the River Ewe stock in Scotland, following a massive intrusion of both juvenile and adult escapes over several years (Butler et al., 2005), no population-level changes in fish size or age of maturation were observed, although a small decrease in age of smoltification was found consistent with a gain in freshwater growth rate. However, actual levels of introgression were not known in the study, and the observations could have been explained by density-dependent changes.

At present, studies considering phenotypic and life-history changes in native populations are effectively lacking (Challenge 2, Figure 3). Thus, there is an urgent need for detailed investigation of both the actual levels of interbreeding and introgression and the phenotypic and life-history changes that arise from admixture with farmed salmon (Figure 3).

4.3 | Will population genetic structure change?

The Atlantic salmon is characterized by widespread structuring into genetically distinct and differentiated populations (Bourret et al., 2013; King, Kalinowski, Schill, Spidle, & Lubinski, 2001; Ståhl, 1987; Verspoor et al., 2005). This is conditioned by the evolutionary relationships among populations (Dillane et al., 2008; Dionne, Caron, Dodson, & Bernatchez, 2008; Perrier, Guyomard, Bagliniere, & Evanno, 2011) and adaptive responses to historical and contemporary environmental differences (Garcia de Leaniz et al., 2007; Taylor, 1991). The largest genetic differences are observed between populations residing on different continents (Gilbey, Knox, O'Sullivan, & Verspoor, 2005; Taggart, Verspoor, Galvin, Moran, & Ferguson, 1995; Tonteri, Veselov, Zubchenko, Lumme, & Primmer, 2009), where chromosome-number differences are also observed (Brenna-Hansen et al., 2012; Lubieniecki et al., 2010). Within continents and smaller geographic regions, population genetic structuring is often, but not always, a function of isolation by distance (Dillane et al., 2007; Glover et al., 2012; Perrier et al., 2011), but is modified by various factors such as colonization history and landscape features (Dillane et al., 2008). Consequently, populations can display genetic differences between regional groups (Bourret et al., 2013), between rivers (Perrier et al., 2011; Tonteri et al., 2009; Wennevik, Skaala, Titov, Studyonov, & Naevdal, 2004) and between tributaries within river systems (Dillane et al., 2007, 2008; Dionne, Caron, Dodson, & Bernatchez, 2009; Vaha, Erkinaro, Niemela, & Primmer, 2007). These genetic differences may be in respect of gene frequencies and variants present at individual loci but may also involve differences in genomic organization as regards aspects such as chromosome structure and number which will affect linkage relationships (Brenna-Hansen et al., 2012) which may have non-additive fitness consequences that are difficult to predict (Cauwelier, Gilbey, Jones, Noble, & Verspoor, 2012).

Simulations have suggested that interpopulation genetic diversity will gradually erode with introgression of farmed escaped salmon (Mork, 1991). Studies of Norwegian populations exposed to farmed escapees have indeed observed a decrease in interpopulation genetic diversity over time (measured as a drop in pairwise or overall F_{ST}) (Glover et al., 2012; Skaala et al., 2006). At the same time, the admixed wild populations became more similar to a pool of Norwegian farmed salmon (Glover et al., 2013). Potential changes in population genetic structure have not been assessed outside Norway. While genetic changes studied so far may be of no functional significance, they may mark general patterns of genomic change, although to what extent this is the case remains an open question. To robustly address this issue, studies of changes in functional genetic variation known to have phenotypic or fitness implications are needed (Consuegra et al., 2005; Coughlan et al., 2006; Ryynanen & Primmer, 2004; Verspoor et al., 2005).

4.4 | Will the severity of impacts vary among wild populations?

Data from empirical studies (Glover et al., 2012, 2013; Karlsson et al., 2016), as well as from models (Castellani et al., 2015; Heino et al., 2015; Hindar et al., 2006), have demonstrated that the levels of introgression are correlated with the number of escapees. This is further modified by the abundance or density of the native population (Glover et al., 2012; Heino et al., 2015), which probably links to spawning and

juvenile competition. Thus, wild populations that are already experiencing natural declines in adult abundance will be more vulnerable to introgression of farmed salmon due to the reduced level of competition faced by the escapees once on the spawning grounds. However, other factors will also condition the level of introgression, and how it varies among populations.

Important factors affecting gene flow and relating to the characteristics of the invading farmed escapees themselves include their body size, the stage at which they escaped and whether they mature as juveniles or adults. Just as important in modifying the competitive success of the farmed escapees will be the biological characteristics of the wild population being invaded. This reaches beyond the density of adults on the spawning ground, but also includes other characteristics such as the predominant sea age of wild returning spawners (i.e. one, two or three sea winters), the propensity for maturation in male parr, and the phylogenetic history of the population. River-specific non-biological factors are also likely to influence the degree of gene flow between farmed escapees and wild salmon. For example, it is likely that rivers with upstream migration challenges (rapids and waterfalls), or large lakes/rivers with smaller tributaries, may hinder the ascent of farmed salmon to higher spawning grounds in some rivers, limiting their scope for interbreeding with wild fish. These biotic and abiotic factors need to be identified to fully understand impacts and which populations are at lesser or greater risk of introgression.

Once gene flow from farmed escapees has occurred, phenotypic, life-history and demographic consequences for wild populations will scale with the level of gene flow. Modifying factors aside, in any given river, increased numbers of escapees will on average increase the probability for introgression and, thereafter, the probability of negative impacts (i.e. changes in life-history and demographics). The level of negative genetic impact may also scale with the degree of domestication and adaptive divergence from wild populations (Castellani et al., 2015). However, the relationship of domestication-driven and ancestry-related divergence with potential for decreases in adult abundance resulting from interbreeding of farmed escapees is not necessarily linear or clear-cut (Baskett et al., 2013). First, the impact on wild population fitness may be at its highest at intermediate genetic divergence between wild and farmed fish (Baskett & Waples, 2013; Huisman & Tufto, 2012), and not when farmed fish resemble wild fish or when they are vastly divergent from wild fish. Second, the effect may depend upon the timing of selection against maladapted farmed fish in relation to spawning (Baskett & Waples, 2013; Baskett et al., 2013). Strongly maladapted escapees may not survive to interbreed with wild populations and, therefore, have no direct genetic impact. However, if selection against farmed fish occurs after spawning, then the negative impact due to hybridization may be severe. Conversely, escapees that are not strongly domesticated, and therefore display a high fitness in the wild, may cause higher levels of introgression than maladapted salmon. However, in such cases, the fitness consequences for the recipient population will not necessarily be as significant, even though qualitative changes in the genetic make-up of the recipient population may occur.

The gradient of divergence between the wild and farmed populations will display differences both regionally and from case to case. For example, farmed salmon are likely to display greater genetic differences to wild salmon in Ireland because of both domestication and non-native origin of the Norwegian salmon that are predominantly farmed there. In contrast, in Norway, the farmed salmon, while displaying domestication-driven differences to the wild salmon, will have originated from the same phylogeographic lineage, except in the Barents sea rivers (Bourret et al., 2013). In Scotland, where both Norwegian and Scottish strains are farmed, the issue will be more complex. Uncertainty about whether greater or lesser divergence from wild populations is better makes it difficult to advise regulators on whether local or non-local farmed strains present a smaller or greater risk if escapes occur (Verspoor, McGinnity, Bradbury, & Glebe, 2015).

A given level of gene flow from farmed salmon is unlikely to elicit the same degree of consequence for all wild populations. Response variation will be controlled by a complicated set of biotic and abiotic population and river-specific factors. Some of the genetic differences between farmed and wild salmon are likely to be population-specific. This includes traits such as growth under different thermal regimes (Harvey, Glover et al., 2016), gene expression patterns (Normandeau et al., 2009), survival and life history in the wild (Fleming et al., 2000; McGinnity et al., 1997; Skaala et al., 2012), competitive balance (Houde et al., 2010a), acid tolerance (Fraser et al., 2008) and pathogen susceptibility (Glover & Skaala, 2006; Lawlor, Dacanay, Hutchings, Brown, & Sperker, 2009). In addition, the competitive balance between farmed and wild salmon may differ with environmental conditions (Fraser et al., 2008; Harvey, Glover et al., 2016; Solberg, Zhang et al., 2013). In addition, the response of F1 hybrids and different backcross types may not always manifest in an additive manner (Debes et al., 2013; Einum & Fleming, 1997; Houde et al., 2010b), and differs among populations (Einum & Fleming, 1997; Houde et al., 2010b). Finally, variation in differences in egg size among the invading farmed escapees and the specific wild population will also influence the competitive balance and potential consequences. Egg size is positively correlated with alevin size (Einum & Fleming, 2000; Solberg et al., 2014) and survival in the wild (Einum & Fleming, 2000; Skaala et al., 2012). In general, farmed escapees display smaller eggs than wild salmon (Lush et al., 2014; Srivastava & Brown, 1991) although egg sizes can vary substantially among populations in the wild and egg size variation may be adaptive (Riddell, Leggett, & Saunders, 1981). However, egg size is positively correlated with female size (Kazakov, 1981; Thorpe et al., 1984). Therefore, even if eggs are smaller for farmed salmon for a given fish size, farmed salmon may produce eggs equal in size to wild fish if the escapees entering the river are much larger than the wild fish (Solberg et al., 2014, 2016). Thus, the effect of phenotypic differences, such as egg size, between escapees, the native population and their subsequent hybrids and offspring will influence the competitive interactions in the wild. These are difficult to predict.

Recent quantitative-genetic simulations have suggested that drip-leakage events (i.e. continuous low level leakage of escapees) are more

likely to cause genetic changes in fitness traits in natural populations than single large-scale escape events (Baskett et al., 2013). Their conclusion contrasted with that of Hindar et al. (2006), who suggested that there is likely to be a greater effect of large pulses of salmon aquaculture escapees on wild populations. This difference arises because of the focus by Baskett et al. (2013) on equilibrium outcomes as compared to Hindar et al.'s (2006) emphasis on short-term dynamics. Despite these differences, the nature of spawning intrusion may have important implications for the fitness of native populations. Closely linked with this aspect is the fact that the pattern of introgression and admixture will have potentially important consequences for the fitness of the native population and, importantly, the ability for natural selection to "purge" admixed individuals out of the population over time. For example, a single massive spawning intrusion in one population in 1 year could theoretically lead to complete hybridization of the population, effectively hindering natural selection to purge admixed individuals out and leaving pure wild individuals (this admittedly represents an extreme hypothetical scenario). In a contrasting scenario, long-term but small-scale intrusion may lead to fragments of the population being wild, hybrid, admixed (backcrossed to wild) and farmed, leaving other opportunities for natural selection to purge maladapted genotypes from the population. The admixture profile of individual salmon in rivers subject to introgression of farmed escapees has not been thoroughly examined thus far. However, there is great potential for this using recently developed statistical approaches to identify individual admixture from diverse domesticated lines (Karlsson et al., 2014). Clearly, differences in individual admixture profiles among populations will also contribute to population-specific impacts and recovery profiles.

4.5 | What are the expected long-term consequences?

The conservation of genetic variation within and among populations (as outlined in the Biodiversity Declaration) is important for the resilience of local salmon stocks to human or natural disturbances (Ryman, 1991; Schindler et al., 2010), and in the long term, reduced genetic variability will affect a species' ability to cope with a changing environment (Lande & Shannon, 1996; McGinnity et al., 2009; Satake & Araki, 2012). Therefore, one-way gene flow, as occurs through the successful spawning of farmed escapees, potentially represents a powerful evolutionary force. It erodes genetic variation among wild populations (Glover et al., 2012) and, in the long run, may also erode the genetic variation within populations under certain situations (Tufto & Hindar, 2003). Wild populations will also become more similar to the less variable farmed populations.

Although evolutionary theory permits us to outline general trajectories, it remains difficult to predict and demonstrate the evolutionary fate of individual wild populations receiving farmed immigrants. The severity and nature of the effect depends on a multitude of factors, including the magnitude of the differences between wild and farmed populations (both historical and adaptive differences), the mechanisms underlying genetic differences between wild and farmed salmon, the frequency of intrusions of farmed fish and the numbers of intruding farmed fish relative to wild spawning population sizes (Hutchings & Fraser, 2008). Furthermore, many wild salmon populations are already under evolutionary strain from a wide variety of anthropogenic challenges (Lenders et al., 2016; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998), and such populations are more likely to be vulnerable to the potential negative effects of genetic introgression. Therefore, genetic introgression must be seen in the context of other challenges.

5 | CONCLUSIONS

5.1 | What have been the largest developments in knowledge in the past decade?

As has been evident throughout this review, much was already known in respect of the potential impact of farmed salmon spawning in the wild on recipient wild populations by the late 1990s and early 2000s. This has provided the regulatory authorities with enough knowledge of potential negative effects of escapees to take appropriate actions. However, at that stage, two major bottlenecks in our capacity to *quantify* the impacts of escapees were still to be satisfactorily resolved, that is, the ability to measure accurately the level of introgression that has occurred, particularly over multiple generations (Challenge 1 – Figure 3), and what the biological consequences are in respect of responses in life history and population abundance and resilience (Challenge 2 – Figure 3).

What critical new knowledge has come to light in the past decade of research? In addition to greater clarity and detail in all aspects linked with escapees and direct genetic interactions, it can be argued that three highly significant advances have been made. Firstly, there is globally unprecedented and unequivocal evidence of introgression of farmed salmon into ~150 native Norwegian populations (ranging from 0% to 47%) (Glover et al., 2013; Karlsson et al., 2016). While this has only been quantified in Norwegian rivers/populations, Norway is currently the world's largest farmed and wild salmon producing country and therefore represents the principal focus of the concern in respect of threats posed by farmed escaped salmon on their wild conspecifics. These studies have moved the debate from "has introgression occurred," to "what is the consequence of this introgression." There is no longer room for doubt regarding the reality of introgression.

The second significant advance in our knowledge is the volume and detail of work on our understanding of the genetic differences that distinguish farmed and wild salmon because of domestication. Approximately half of the studies addressing this have been conducted in the past decade. These do not only provide us with knowledge that furthers our understanding of the potential consequences of genetic interactions, they provide us with a better understanding relating to the underlying mechanisms. Furthermore, this knowledge is highly transferrable to other aquaculture systems where genetic interactions between cultured and wild organisms can occur (Araki & Schmid, 2010). These non-salmonid aquaculture systems can use the salmon as the "model system" to understand genetic interactions

between farmed escapees and wild conspecifics (Bekkevold et al., 2006). Finally, but not least, the results of these studies have provided breeding companies with unique insights into the changes elicited by their selective regimes. In turn, this may help adjust future breeding plans and approaches.

The third major recent advance has been the development of genomic resources, especially the recently published salmon genome (Lien et al., 2016). While the potential of the entire salmon genome sequence has yet to make a major contribution (but see its immediate impact on our understanding of maturation (Ayllon et al., 2015; Barson et al., 2015)), other genomic developments such as high-density SNP chips and linkage maps together with transcriptomics tools have underpinned some of the recent advancements detailed above. For example, a SNP chip was instrumental in the discovery of genetic markers that permit identification of farmed and wild salmon irrespective of their population or strain of origin (Karlsson et al., 2011), which have thereafter been used to quantify introgression (i.e. the single biggest advance). These recently and continuously emerging genomic resources now provide us with opportunities that were previously impossible.

5.2 | What major questions remain unanswered?

There are two broad and vitally important questions that remain to be fully elucidated in the grand scheme of things: 1. the current lack of unequivocal documentation and quantification of the biological consequences (productivity and abundance, resilience, life-history profiles) of introgression in natural populations (challenge 2 – Figure 3) and 2. our knowledge of and the potential need to establish threshold tolerance limits, if they exist. These are discussed briefly below.

It is well documented that farmed and wild salmon differ in many phenotypic traits (Tables 1-9). Also, there is experimental evidence showing negative fitness effects of introgression by farmed fish into wild populations. However, there is still a lack of documentation of the biological changes in natural populations at present. This can be broken down into the following interrelated questions: a) To what extent have biological changes occurred in wild populations following direct genetic interactions with farmed escapees? b) Among the many traits at which farmed and wild salmon differ, which are the ones that contribute the most to fitness loss in introgressed populations? c) How and how fast can natural selection purge maladaptive variation from recipient wild populations if farmed escapes could be minimized or discontinued? d) What is the genetic architecture (genome, transcriptome, epigenome) of traits important for fitness in the wild? The sequencing of the genome and the rapidly emerging genomics tools described above provide valuable resources for addressing these challenges.

Mining farmed-wild diagnostic loci from genomic data (Karlsson et al., 2011) now provides us with vastly improved ability to compute admixture in individual fish and connect these estimates together with ecological and biological (i.e. phenotypic traits) measurements in the wild. This will help us unravel and quantify the population-level impacts. Furthermore, monitoring adaptive genetic change can be conducted by analysing time series of samples from wild populations using high-resolution genomic methods (e.g. dense SNP chips) (Hansen, Olivieri, Waller, Nielsen, & Ge, 2012). By analysing multiple temporal samples before, during and after events of escapes and introgression it would be possible to identify loci where alleles derived from farmed salmon are under strong negative selection in the wild and follow their fate from introgression to possible purging. This would permit us to start quantifying the strength of natural selection to purge and/or naturalize farmed salmon and their hybrids in natural populations where introgression has occurred. Thus, it is likely that within the near future, the process of addressing and answering one of the most significant questions, that is what biological changes have occurred because of introgression, should emerge.

Once biological changes have been documented and quantified, there will arguably be one more question, and perhaps the "ultimate" one remaining which concerns defining possible tolerance threshold limits. Do wild populations display the evolutionary plasticity (both genetic and environmental) to absorb for example 1%, 5% or 10% introgression of farmed escapees without changing their key parameters (life-history and demographic), and without losing future evolutionary potential to other challenges such as climate change and further anthropogenic forces? It is beyond the scope of this review to evaluate mitigation strategies, but, to our knowledge, Norway is the first and only country in the world to establish threshold limits of "sustainability" linked to the frequency of farmed escapees and genetic impact on the native population (Taranger et al., 2015). The established thresholds for the incidence of farmed escapees in a wild population were set for <4% (no to low), 4%–10% (low to moderate) and >10% (high) probability of genetic change in the wild population, respectively. These threshold categories were established using a "best guess" based on current knowledge. They remain, however, scientifically unvalidated. Approaches to answer this question have been to relate the allowable amount of gene flow between cultured and wild salmon to the observed level of genetic differentiation occurring between them (Ryman, Utter, & Hindar, 1995). For most levels of genetic differentiation observed among salmon populations, this would translate into low numbers of migrants between them. For subspecies of cutthroat trout (*Oncorhynchus clarki*, Salmonidae), some have argued that there is no other defensible limit on genetic introgression than a very small one (Allendorf et al., 2004).

5.3 | Summary and scientific recommendations

I. *Spawning success of farmed escapees, and how this varies in time and space, requires further quantification to predict introgression.* Experiments show that adult escapees have reduced spawning success compared to wild salmon that depends on the life stage at which they escape into the wild, mature, and attempt to spawn with wild fish, and the level of competition with wild fish on the spawning grounds. Furthermore, farmed females display a greater relative spawning success than farmed males, which will increase the relative frequency of hybrid as opposed to pure farmed offspring.

Farmed escapee sperm and egg quality appears equal to that of wild adults, but farmed females tend to produce eggs that are smaller than wild eggs when corrected for body weight. However, whether the offspring of farmed or hybrid salmon that have lived their entire lives in the wild will always have a lower reproductive fitness than wild salmon remains unclear.

II. *There is a need to use molecular-genetic markers to quantify introgression in populations, especially in knowledge poor regions.* Introgression of farmed salmon is documented in many Norwegian populations and varies greatly among studied rivers (0%–47%), but remains largely unquantified elsewhere. Using molecular markers to quantify introgression, and accurately compute individual admixture, depends upon markers being diagnostic for farmed fish. This is affected by factors such as the ancestry of the specific farmed strains and wild populations involved. A better understanding of the genomic basis of domestication would help to identify better markers. At the same time, better insights into how biotic (wild population characteristics) and abiotic (river temperature, length, gradient, number of upstream migration challenges) factors influence introgression would help us to identify populations most at risk.

III. *The genetic differences between farmed and wild salmon that affect fitness need to be better understood to predict the impact of introgression.* A wide number of differences in genetic-based phenotypic traits have been observed between farmed and wild salmon including those associated with selection for economic and domestication traits. As not all trait differences may influence fitness in the wild, there is a need to identify which traits have the most negative impact in any given wild population subject to introgression.

IV. *Further information is needed on the fitness of farmed, admixed and wild salmon in different rivers, either using planting experiments that combine genetic and ecological measurements, or by monitoring offspring following spawning intrusions, and on selective change.* Only two whole-generation studies have been conducted in the wild, producing estimated relative fitness of farmed salmon to be 2%–16% that of wild salmon. A further study has demonstrated that the offspring of farmed salmon may display relatively high, though still lower, survival in the freshwater stage. However, the relative survival of farmed salmon offspring in the wild is likely to vary from case to case.

V. *Biological consequences (life-history, phenotypic and demographic) of farmed salmon introgression have been inadequately studied in the wild.* An increase in within-population genetic variation and a simultaneous loss in genetic diversity among populations have been observed in Norwegian populations exposed to gene flow from farmed escapees. A combination of empirical data from laboratory and field experiments together with evolutionary theory and synthesis through models suggest that when exposed to gene flow from farmed escapees, genetic changes in wild populations will occur in the direction of the invading farmed strains in phenotypic and life-history traits. Furthermore, as the offspring of farmed salmon compete with wild salmon for resources in the river, introgression will also lead to a reduction in the production of wild (two wild parents) smolts, as well as a potential reduction in the total number of smolts and returning adults (all genetic backgrounds). Detecting population-level changes will be challenging in the short-term and under low-to-modest introgression scenarios because wild populations are plastic in their phenotypic and life-history responses. Together with environmental stochasticity, this will tend to mask early changes. Also, the force of natural selection to purge maladapted genotypes from native populations following introgression remains to be quantified. This makes it imperative to undertake *in situ* studies and to have a commitment to long-term, pedigree-based, longitudinal studies of natural populations.

VI. *Evaluation of direct genetic impact of farmed escapes on wild populations must be seen in the context of additional challenges.* The genetic impact of escapees on the genetic integrity and long-term evolutionary capacity of native populations will scale with the numbers of escapees entering the rivers, in addition to each population′s specific characteristics. This effect may interact negatively with other challenges faced by these populations such as climate change, disease and pathogen challenges, habitat loss, overfishing, acidification.

VII. *The long-term consequences of introgression on native populations can be expected to lead to changes in life-history traits, reduced population productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).* Conducting research on various aspects of the genetic interactions between farmed escapees and wild conspecifics is crucial to understand mechanisms, quantify impacts, determine resiliency and estimate the recuperative potential of wild populations. Such research will, however, not solve the problem. This requires additional research into impact avoidance or mitigation strategies that can hinder or stop further erosion of genetic integrity. Finally, it is important to make it unequivocally clear that only a substantial or complete reduction in the number of escapees in rivers, and/or creating a reproductive barrier through sterilization of farmed salmon, will represent a solution to the challenge.

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