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Genetic improvement technologies to support the sustainable growth of UK aquaculture

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Abstract
While the UK is the fourth largest aquaculture producer in Europe by volume, it is the second largest by value with an annual first sale value of around £1 billion. Over 90% of this value is from Atlantic salmon farmed in Scotland, but other fish and shellfish aquaculture species are important to several UK regions. In this review, we describe the state of the art in UK aquaculture breeding and stock supply, and how innovation in genetics technologies can help achieve the Scottish Government’s ambitious target of doubling its aquaculture industry by 2030. Particular attention is given to the four most important UK aquaculture species: Atlantic salmon, rainbow trout, blue mussel and Pacific oyster, and we contrast the highly variable level of selective breeding and genomics technologies used in these sectors. A major factor in the success of Atlantic salmon farming has been large-scale investment in modern breeding programmes, including family selection programmes and genomic selection. This has proven cost-effective at scale, leading to improved production efficiency and reduction of some infectious diseases. We discuss the feasibility of applying similar technologies to the UK shellfish sectors, to ensure consistent and robust spat supply and begin trait selection. Furthermore, we discuss species-specific application of modern breeding technologies in a global context, and the future potential of genomics and genome editing technologies to improve commercially desirable traits. Increased adoption of modern breeding technologies will assist UK aquaculture industries to meet the challenges for sustainable expansion, and remain competitive in a global market.

Key words: Atlantic salmon, blue mussel, genome editing, genomics, industry benefits, Pacific oyster, rainbow trout, selective breeding.

Introduction
Aquaculture is the fastest growing farmed food production sector globally (FAO 2020b) and is an important component of the UK economy. The UK aquaculture industry supports employment in remote rural and coastal areas of the Scottish Highlands and Islands, in addition to deprived urban areas where much processing takes place (Alexander \textit{et al.} 2014; Munro 2019; Munro 2020). The UK is the fourth largest aquaculture producer by volume in Europe (5% of total European production) but is the second largest by value with a production value of over £1 billion in 2018 (FAO 2020a). With its fractal coastline measuring over 31 000 km and stretching from warm temperate to cold temperate zones (Marine Management Organisation 2013), the UK provides abundant access to diverse marine environments, and to extensive freshwater resources. This range of conditions provides opportunities to culture a diversity of species, but also the challenge of identifying species most suited to a given region and environments. An example of successful exploitation of the amenable environment is the west coast of Scotland where sea lochs provide sheltered areas of seawater, ideal for salmon farming (Black & Hughes 2017). In fact, farmed Atlantic salmon alone contributed >90% of UK aquaculture production value (FAO 2020a). Since the first UK farm was established in Scotland...
in the late 1960s (Munro et al. 1979), salmon farming has become a very successful industry, both nationally and globally. The success of UK salmon farming is attributed to many factors, including technical advances in culture systems, for example recirculation aquaculture systems (RAS) for smolt production, husbandry methods, improved control of the lifecycle to ensure year-long supply, advances in feeds and nutrition, better health management, and domestication and breeding of improved strains. These advances have been facilitated by industry consolidation, economies of scale, vertical integration and international cooperation (Ellis et al. 2016).

The early uptake and widespread adoption of well-managed selective breeding programmes have been key to this success for Atlantic salmon, with cumulative improvements in growth performance and traits such as disease resistance (Gjedrem & Rye 2018). However, the level of sophistication of genetic technologies varies hugely between species, and these technologies are both advancing rapidly and becoming more affordable and accessible (Houston et al. 2020). Therefore, there is likely to be significant untapped potential to improve other sectors of UK aquaculture production and sustainability via innovation and implementation of genetics and breeding technologies. Uptake of these technologies across species sectors is essential for the UK to remain competitive in a global market, and to tackle some pressing challenges currently facing the industry. This review gives an overview of the current status of the major UK aquaculture species, compares selective breeding strategies used for these species in the UK versus the global state of the art in breeding technologies and outlines current and future challenges, together with technical developments and breeding strategies that can help meet these challenges.

The state of UK aquaculture

Four species dominate UK aquaculture, together accounting for over 98% of production volume and value: *Salmo salar* (Atlantic salmon), *Mytilus* sp. (blue mussel), *Oncorhynchus mykiss* (rainbow trout) and *Crassostrea gigas* (Pacific oyster) (Table 1). The political, regulatory, media and technical interests of the industry sectors for the main farmed species are represented by separate trade bodies: most salmon production is represented by the Scottish Salmon Producers Organisation (SSPO); The British Trout Association represents 80% of UK trout production; The Shellfish Association of Great Britain is composed of shellfish farmers, fishermen, fishermen associations, processors, commercial traders and retail companies (Carvalho et al. 2018). The features of the production systems for each of these four main aquaculture species are discussed below.

Atlantic salmon (*Salmo salar*)

Atlantic salmon, the UK’s biggest food export (FDEA 2020), is by far the most valuable aquaculture species in the UK. The UK is the third largest producer of Atlantic salmon in the world (after Norway and Chile) with almost all of its farms based in Scotland (Black & Hughes 2017). Due to the diverse lifecycle requirements, high feed and capital costs, and time to harvest (Fig. 1), salmon are typically farmed by large multinational companies. A benefit of this structure is that industry investment in research and development is significant, which extends to selective breeding technology. Although over 24 companies are involved in hatchery rearing, smolt production and sea farming of salmon in the UK (Munro 2019), five were responsible for 94% of the total harvest in 2018: Mowi (formerly Marine Harvest), Scottish Sea Farms, The Scottish Salmon Company, Cooke Aquaculture and Grieg Seafood (Mowi 2019).

Rainbow trout (*Oncorhynchus mykiss*)

Native to northwest America, rainbow trout were introduced to Britain in the 19th century (Nash 2011). Adaptable to many environments, these hardy fish are relatively easy to breed, saltwater tolerant and suitable for cultivation. Although rainbow trout farming expanded rapidly in the UK during the 1980s, it has remained at an almost constant and relatively low level since (Hambrey & Evans 2016). Similar to Atlantic salmon, rainbow trout undergo multiple life stages, each requiring different husbandry and management (Fig. 1). Historically, rainbow trout were harvested at portion size (ca 400 g). However, the price of larger fish is generally higher (Hambrey & Evans 2016), leading to an increase in rainbow trout marine net-pen farms growing fish to a similar harvest size as Atlantic salmon. Over half of the rainbow trout tonnage produced in Scotland is now grown in sea lochs, similar to Atlantic salmon (Munro 2019), making up a quarter of total UK rainbow trout production volume since 2014 (FAO 2020a). In the UK, the majority (90%) of trout farmed for the table and stocking waters for angling are produced by members of the British Trout Association (Robinson 2015), comprising over 50 farming companies mostly in Central and Southern Scotland, Southern England and North Yorkshire. Many of these members are directly affiliated with large multinational breeding companies.

Blue mussel (*Mytilus spp.*)

Compared with finfish, shellfish aquaculture is relatively small scale across the UK, representing 11% by weight of all marketed species (~22 000 tonnes) and valued at around £36 million (Table 1). However, mussel farming is the
Table 1  Annual UK aquaculture production tonnages, by region averaged over the period 2013–2018 with farm gate values imputed from estimates of unit value (£/tonne). Tonnages reported by producers excludes production of ova, juveniles and ornamental fish reported by number. Finfish caught in sport angling typically consumed, while those caught in coarse angling released; Shaded species represents harvest of wild self-seeded production from shellfish aquaculture sites. ‘nei’ (not elsewhere included) is used to combine production of minor species and anonymize confidential figures. Source: Cefas compilation of UK statistics for Eurostat and FAO

| Species & use of production | Sea/fresh water | Scotland | England | Wales | Northern Ireland | UK total | % | £ value |
|-----------------------------|----------------|----------|---------|-------|-----------------|----------|---|---------|
| **Finfish – consumption, sport angling & cleaner fish** | | | | | | | | |
| *Salmo salar* Atlantic salmon | SW | 170 421 | 7 878 837 562 | 52.34 | 16 226 616 | 216 839 645 | 639 | 2 609 358 | 170 421 | 82.34% | 787 837 562 | 90.41% |
| *Oncorhynchus mykiss* Rainbow trout | FW, SW | 7038 | 18 917 829 | 0.1 | 1847 | 449 | 2 968 590 | 460 | 0.22% | 3 198 630 | 0.37% |
| *Salmo trutta* Brown trout | FW | 42 | 1 197 743 | 11 | 82 181 | 84 | 376 500 | 84 | 0.04% | 376 500 | 0.04% |
| *Dicentrarchus labrax* European sea bass | SW | 45 | 158 795 | 45 | 0.02% | 158 795 | 0.02% |
| *Oreochromis niloticus* Nile tilapia | FW | 41 | 504 900 | 0 | 41 | 504 900 | 0.06% |
| *Hippoglossus hippoglossus* Atlantic halibut | SW | 30 | 263 164 | 30 | 0.01% | 263 164 | 0.03% |
| *Salvelinus alpinus* Arctic char | FW | 12 | 64 803 | 12 | 0.01% | 64 803 | 0.01% |
| *Cyprinus carpio* Common carp | FW | 5 | 74 298 | 5 | <0.01% | 74 298 | 0.01% |
| *Cyprinus carpio* (inc. hybrids) Lumpfish | SW | 2 | NA | 2 | <0.01% | NA |
| *Labrus bergylta* Ballan wrasse | SW | 0.54 | NA | 1 | <0.01% | NA |
| *Osteichthyes* Freshwater fish nei | FW | 0.2 | 2438 | 0.01% | 274 | 0.01% | 2438 | 0.01% |
| **Finfish – coarse angling** | | | | | | | | |
| *Cyprinus carpio* Common carp | FW | 160 | 2 325 343 | 0.1 | 1 148 | 160 | 0.08% | 2 326 491 | 0.27% |
| *Osteichthyes* Freshwater fish nei | FW | 25 | 529 377 | 0.04% | 609 | 25 | 0.01% | 529 986 | 0.06% |
| **Finfish total** | | | | | | | | |
| *Mytilidae* Blue mussel spp | SW | 177 574 | 8 076 463 | 57.20 | 21 314 139 | 3 116 287 | 1088 | 5 579 380 | 184 694 | 89.24% | 835 840 756 | 95.92% |
| *Crassostrea gigas* Pacific cupped oyster | SW | 7425 | 9 023 706 | 1979 | 3 116 287 | 5295 | 8 593 765 | 3113 | 8.61% | 24 457 056 | 2.81% |
| *Ostrea edulis* European flat oyster | SW | 274 | 1 278 792 | 596 | 2 305 744 | 15 | 34 233 | 631 | 0.91% | 5 430 257 | 0.62% |
| *Pecten maximus* Great Atlantic scallop | SW | 17 | 123 750 | 12 | 54 008 | 29 | 0.01% | 177 758 | 0.02% |
| *Aequipecten opercularis* Queen scallop | SW | 5 | 66 764 | 5 | <0.01% | 66 764 | 0.01% |
| **Crustacea – consumption** | | | | | | | | |
| *Litopenaeus vannamei* Whiteleg shrimp | SW | 7724 | 10 503 761 | 5496 | 10 887 509 | 5309 | 8 627 999 | 3745 | 0.91% | 35 555 882 | 4.1% |
| **Shellfish total** | | | | | | | | |
| **Finfish & shellfish total** | | | | | | | | | | | | |
second largest aquaculture sector by production volume in the UK after salmon. UK mussel farming relies entirely on collection of wild spat, either by natural settlement on ropes, or by harvest from natural mussel beds before on-growing in farms (Fig. 1; Adamson et al. 2018). The main species cultivated is the native blue mussel, *Mytilus edulis*, although hybridization with Mediterranean (*Mytilus gallo-provincialis*) and soft-shelled or foolish (*Mytilus trossulus*) mussels is present in Scottish farms (Dias et al. 2009). This latter hybridization has been associated with less desirable commercial traits such as reduced yield and softer shells (Michalek et al. 2016). Mussels filter-feed on wild phytoplankton and particulate organic matter without requiring additional feed input. The farming cooperative, the Scottish Shellfish Marketing Group, trades most of Scotland’s mussel crop with members throughout Scotland. The Shetland region provides the greatest contribution, accounting for 80% of Scotland’s total harvest in 2019 (Munro 2020). All mussel farming in Scotland is on suspended raft and long-line systems, which depend on natural settlement of spat. Elsewhere in the UK, bottom cultivation is also practised. The Menai Strait in Wales was historically the largest mussel producing area in the UK. Following spat collection, mussels are grown on the intertidal bed of the Menai Strait over roughly 10 km². In recent years, production has fallen below that of Scotland, due to a low availability of mussel seed (Addison 2018). Offshore Shellfish Ltd., situated in Brixham, Devon recently developed the first fully offshore, large-scale, suspended rope grown farm in the UK (Antrobus 2017). At full production capacity, the 15.4 km² farm aims to harvest around 10 000 tonnes of mussels each year from its three offshore sites in Lyme Bay. This production is predicted to offset the recent decline in UK mussel production (STECF 2018).

**Pacific oyster (*Crassostrea gigas*)**

Unlike mussel farming, Pacific oyster (also known as the Japanese oyster) farming in the UK is dependent on hatchery sourced oyster spat. A non-native species from the North West Pacific, *C. gigas* constitutes the bulk of hatchery-produced bivalves in the UK at present. Most oyster farmers in the UK are supplied by one of two oyster hatcheries – Guernsey Sea Farms in the Channel Islands and Morecambe Bay Oysters, Lancashire (Adamson et al. 2018). Hatcheries in the UK do not currently run selective breeding programmes. The developing larvae are provided with warm-temperate water and algal feeding systems for the first few months of the life cycle. The feed is produced using a combination of indoor high-density microalgal systems and inoculation and blooming of outdoor ponds. The production of large volumes of several microalgae species to fulfil larval and spat nutritional requirements represents the bulk of production costs for UK oyster hatcheries. This
results in a higher seed cost than mussel farming, although oysters reach a higher market value per weight (Table 1). UK growers begin their phase of oyster culture with spat, several months old, which are commonly maintained in bags or in cages elevated from the seabed on trestle structures (Adamson et al. 2018). The growing oysters are regularly inspected for damage, graded for size and turned to ensure even access to food and the development of a uniform, deep cupped shell. They are typically on-grown for one to three years before harvest (Fig. 1).

Atlantic salmon

Fertilized ova are typically incubated to eyed stage (from 250 °days) by the breeding company and then transferred to RAS or flow through (FT) salmon hatcheries (usually at 400 °days) where they hatch (500 °days), first feed (from 850 °days) and become parr (from 1500 °days to 5 g). This takes 16–24 weeks. Fish are then on-grown in either RAS or freshwater (inc. loch net-pens) and undergo the parr–smolt transformation also known as smoltification. This process occurs naturally (from August of year 1 to April/May of year 2), or may be controlled for out of season transfer to seawater. Smoltification manipulation is done using standardized photoperiodic regimes (400 °days of simulated short days followed by 400 °days of long days). It takes 5–11 months from parr (5 g) to seawater transfer (80–150 g) depending on smolt cohort produced (usually known as quarter of the year) and systems used (RAS or ambient/FT). Fish are then on-grown in seawater pens, traditionally in sea lochs but also more exposed locations in the Scottish western isles and harvested 1–2 years after marine transfer at a harvest weight of 4–5 kg (Mowi 2019). Rainbow trout: Fertilized ova from selected locations in the Scottish western isles and harvested 1 pens, traditionally in sea lochs but also more exposed (RAS or ambient/FT). Fish are then on-grown in seawater (usually known as quarter of the year) and systems used (RAS or ambient/FT). Fish are then on-grown in seawater pens, traditionally in sea lochs but also more exposed locations in the Scottish western isles and harvested 1–2 years after marine transfer at a harvest weight of 4–5 kg (Mowi 2019).

UK aquaculture, breeding and genetic technologies

In the past decade, worldwide production from aquaculture has grown rapidly and overtook capture fisheries in 2018 (FAO 2020b). In the UK, however, aquaculture production growth is substantially lower than the global rate (Fig. 2), despite governmental and industry aspirations for expansion and abundant evidence of the contribution to the UK economy and food security (Alexander et al. 2014). Development of aquaculture in England, Wales and Northern Ireland has been stagnant or declining for many years (Hamrey & Evans 2016). Plans for the sustainable development of aquaculture in the UK have been published (DEFRA 2015), and aquaculture development within England is currently being addressed within The Seafood 2040 Strategic Framework (Seafood 2015). The Scottish government stated their support to double aquaculture production and economic contribution from £1.8 billion in 2016, to £3.6 billion, and double the number of jobs to 18 000 by 2030 (The Scottish Government 2017). To achieve these ambitious goals, there are a number of challenges that must be addressed. Current obstacles to expansion include concerns about environmental impact, animal welfare, disease outbreaks, social licensing, limitations in site availability and size, oyster and mussel seed supply, public perception and competition with other sectors such as tourism and agriculture. On top of this, climate change is likely to bring stormier coastal environments, less predictable plankton blooms including harmful jellyfish and algae (Moore et al. 2008; Carvalho et al. 2018), changes in seawater temperature, freshwater availability (rainfall), salinity and acidity. Furthermore, each of these factors is likely to add to the burden of emerging or novel pathogenic diseases and influx of non-native invasive species. These challenges are all interlinked and will require significant innovation and investment to overcome them.

Two factors limiting expansion are site availability with adequate water quality and carrying capacity, and in the case of finfish, environmental impact. However, increased development of offshore or more exposed net-pen facilities, and recirculating aquaculture systems (RAS) on land and semi-contained at sea (Black & Hughes 2017) could overcome many of the issues associated with space
requirements, and reduce environmental impact (James & Slaski 2006). Additionally, growing larger size smolt and post-smolt on land to reduce time spent in marine net-pens and enabling more frequent harvests has been further enabled via introduction of RAS (Carvalho et al. 2018).

Typically, aquaculture feed (aquafeed) comprises 50–60% of the operating costs for a finfish production business (Black & Hughes 2017). During the last two decades, a trend towards changing the formulation and sourcing of aquafeeds with more sustainable products, using less fish meal (FM) and fish oil (FO) has been a priority (Napier et al. 2020). This trend is likely to continue (Kok et al. 2020), posing the challenges of maintaining good health and performance of the fish as they adapt to these new diets including antinutritional factors (Glencross et al. 2020; Vera et al. 2020), and increased competition for land to grow raw ingredients.

Since most farming takes place in open systems and at high stocking densities, pathogens from wild reservoirs of disease are difficult to avoid and can spread rapidly (Yáñez et al. 2014a). Infectious disease is estimated to cause a loss of 10% across all cultured aquatic animals, amounting to >10 billion USD annually on a global scale (Evensen 2016). Control of the frequent emergence of previously unknown pathogens is made more difficult by the lack of knowledge surrounding background microbial diversity in farm systems (Stentiford et al. 2017). This has led to calls for improved ‘pathobiome’ definitions, to better understand microbial communities affecting the health of farming environments rather than focusing on single pathogens as disease causing agents (Gilbert et al. 2016; Bass et al. 2019). In particular, this highlights the need for improving the overall resilience of the farmed animals to better withstand challenges from multiple pathogens.

Figure 2  Production volume of aquaculture versus capture fisheries (a) worldwide and (b) in the UK (FAO 2020a).
Selective breeding will have a significant role to play in most of the aforementioned challenges (prevention of disease, adaptation to vegetarian diets, reducing environmental impact and adapting to climate change) (Gjedrem et al. 2012). For example, host resistance to many aquaculture pathogens is demonstrably heritable (Ødegård et al. 2011; Yáñez et al. 2014b; Gjedrem 2015), meaning breeding of stocks with enhanced resistance is feasible. As UK aquaculture expands, selective breeding can also play a key role in the adaptation of a given species or strain to different locations, environments, aquafeeds and rearing techniques, for example RAS, and in improving the overall efficiency of production for a given environmental impact. Selective breeding may also be used synergistically with other approaches to improve aquaculture, such as environmental programming, functional feeds or preventive disease treatments. For example, to reduce cost and increase sustainability, fish can be selectively bred for the ability to thrive on plant-based feeds (Quinton et al. 2007; Callet et al. 2017).

Genetic improvement via selective breeding

In order to sustain healthy and productive aquaculture systems, a reliable supply of good quality stocks is required. Compared with terrestrial farm animals and crops, which have typically been domesticated over hundreds or thousands of years, domestication of aquaculture species is in its infancy (Teletchea & Fontaine 2014; Yáñez et al. 2015). Therefore, there remains a high level of genetic variation in aquaculture species across strains, lines, families and individuals (Abdelrahman et al. 2017). Well-managed breeding programmes can maintain and harness this genetic variation to improve production traits in a sustainable manner. For example, finfish breeding programmes have demonstrated that genetic gains in economically important traits of 10–14% per generation can be achieved (Gjedrem et al. 2012). These gains are substantially higher than those typically reported in terrestrial livestock (Hickey et al. 2017). Traits such as growth and disease resistance have as much as 0.3–0.6 and 0.1–0.5 heritability, respectively (Duncan et al. 2013). However, to harness this genetic variation to improve production requires significant investment in selective breeding technology. Approximately 75% of production of the top 10 global finfish, crustacean and mollusc species (Houston et al. 2020), and 80% of all European aquaculture production by volume benefit from some form of modern selective breeding programme (Janssen et al. 2017). However, a wide range of breeding technologies are used by different sectors, from reliance on wild seed/fish stocks, to family-based selection augmented with use of genomic tools. This variation can clearly be observed in the UK; the mussel industry relies entirely on wild spat for production, while Atlantic salmon aquaculture employs the highest level of technology, including advanced trait recording and routine use of genomic selection for multiple traits in selection indices. A parallel may be drawn here with Chile, which has similar divergence in the level of breeding technologies used across its salmonid and mussel aquaculture sectors (Lhorente et al. 2019; FAO 2020b).

The terminology involved with several aspects of genetic technologies and breeding strategies can appear quite complex. Box 1 provides definitions for the breeding tools and technologies, which we refer to throughout this review. Selective breeding programmes are based on selecting the best individuals to breed from, according to records of traits of interest measured in the broodstock and/or relatives, together with tracking of genetic relationships via pedigree recording or use of genetic markers (typically 100–450) for post-hoc reconstruction of pedigrees (Van-deputte & Haffray 2014). Family-based selection requires the traceability of family origin, and is used to maximize genetic gain without the risk of inbreeding depression, that is avoiding expression of recessive deleterious mutations (Charlesworth & Willis 2009). This method of selection has long been used in salmon breeding (Gjedrem 2010). Individual tagging and tracking is performed using Passive Integrated Transponder (PIT) tags, physical marks, or post hoc parentage assignment with genetic markers. In addition to minimizing inbreeding, tracking of pedigree allows recording and improvement of traits which cannot be measured easily in the selection candidates themselves, such as disease resistance, feed conversion efficiency, environmental tolerance and product quality (Yáñez et al. 2015). For these traits, the EBVs of their siblings are used in a process known as sib-testing or sib selection (Box 1). As such, for these traits, breeding values can only be estimated at the family level without genomic data and therefore do not capitalize on the within-family, or Mendelian sampling component of genetic variation (Hill 2013).

In the sib-testing schemes described above, improvements in selection accuracy can be achieved via the use of genetic markers associated with variation in the phenotype of interest. There are two main routes by which this can be achieved: marker-assisted selection (MAS) and genomic selection. In both cases, it is important to first determine the genetic architecture of the trait in question; specifically whether it is controlled by single or few quantitative trait loci (QTL) of large effect, or many QTL of small effect.

Marker-assisted selection involves the detection and use of genetic markers linked to specific QTL affecting the trait of interest, and has been applied to several aquaculture species worldwide including Atlantic salmon and rainbow trout grown in the UK (Yue 2014; Liu et al. 2018; Shen & Yue 2019; Houston et al. 2020; Fraslin et al. 2020). By identifying genetic markers, usually SNPs, which segregate non-
randomly with QTL, one may employ marker-assisted selection to enhance family-based selective breeding at relatively low additional cost. However, for this to be effective, it is important that the specific QTL targeted have a large effect, and are consistent in their effect across families and populations. Encouragingly, there are notable examples of where this is the case. In the case of delaying sexual maturity, two independent studies identified the gene vgll3 being responsible for 33–39% of the phenotypic variation (Ayllon et al. 2015; Barson et al. 2015). Another desirable trait is disease resistance, (Moen et al. 2007; Yañez et al. 2014a; Gonen et al. 2015) and one of the most successful cases of breeding for disease resistance using MAS is that of infectious pancreatic necrosis virus (IPNV). Here, one major QTL was identified as being responsible for 29% of the observed phenotypic variance in disease resistance (Houston et al. 2010). Using this information, MAS was effective in reducing disease incidence in freshwater salmon fry from 47% to 9% in one year alone (Norris 2017). This discovery and subsequent implementation is estimated to have saved £26.4 million gross value added (GVA) per year and 750 jobs in the Scottish salmon industry (Houston et al. 2010). Similar techniques are being tested to tackle other major diseases affecting the UK aquaculture industry at present such as Oyster Herpes virus (OsHV-1) resistance in Pacific oysters (Gutierrez et al. 2018a) and resistance to
the Bonamia parasite which is the biggest challenge to Ostrea edulis (flat oyster) cultivation at present (Vera et al. 2019).

Genomic selection (GS) expands on MAS by utilizing genome-wide markers (usually SNPs) to predict genomic breeding values (GBVs) for selection candidates (Box 1). It is based on the theory that with sufficient numbers of loci across the genome, most QTLs will be in strong linkage disequilibrium with at least one marker (Meuwissen et al. 2001). The estimated breeding value for a given trait is calculated by taking into account the combined effects of all markers, and these are estimated in a training population where all animals are genotyped and measured for traits of interest. The data from the training population are used to train the genomic prediction statistical model which is then applied to calculate breeding values for selection candidates. As such, while MAS is more affordable, GS is particularly useful for breeding oligo- or polygenic traits, that is traits influenced by many loci of relatively minor effect such as growth and resistance to most diseases, overcoming many of the limitations associated with MAS (Zenger et al. 2018). The efficacy of genomic selection can be assessed by using the genomic prediction model to predict traits in a test population in which trait values are known but masked, often using a process known as cross-validation (Zenger et al. 2018). To date, the use of genomic selection has resulted in higher prediction accuracy of breeding value than pedigree information alone for every aquaculture species it has been applied to including Atlantic salmon (Yanez et al. 2015) and rainbow trout (Vallejo et al. 2017). One of the reasons for the improvement accuracy is that genomic relationships estimated by genetic markers can capture realized relationships between individuals rather than the approximations used in a pedigree-based relationship matrix. For example, while traditional additive genetic matrices assume a relationship between full siblings of 0.5, the realized relationship between pairs of full siblings varies substantially around this mean, in theory from 0 to 1 (Ødegård & Meuwissen 2012).

Transformative rearing technologies and husbandry regimes are integral to realizing the benefits of breeding programmes by ensuring optimal performances of the stocks. For example, cryopreservation of finfish milt (sperm) (Cabrita et al. 2001; Yang et al. 2018) and bivalve larvae (Suquet et al. 2014; Rodriguez-Riveiro et al. 2019) enables long-term storage of genetic material from optimal selection candidates. The high fecundity of aquatic species means that genetically improved stock can be disseminated from a single nucleus to a broad geographical and environmental range. Other innovations include the photoperiod manipulation of parr–smolt transformation (smolification) and early maturation during the first year at sea, and land based RAS. There is a global trend for adopting RAS more universally for aquaculture (Espinal & Matulić 2019), and they are likely to become more important in the UK. For example, most rainbow trout farming in Denmark is now performed in RAS, largely driven by strict environmental legislation (Jokumsen & Svendsen 2010). While minimizing water use and reducing effluent discharge, adoption RAS in farming practice also enables a full control of the environment, minimizing exposure to pathogens. Additionally, this environmental control could improve production traits and mitigate potential health and welfare issues through early life programming. Early-life experiences associated with, for example feed, temperature and microbiome can have long-term impacts on performance, robustness and welfare of farmed stocks (Clarkson et al. 2017; Vera et al. 2017; Martos-Sitcha et al. 2020). These effects are largely attributed to epigenetic modifications, that is changes that do not alter DNA but can regulate gene expression, which can in some cases be retained not only later in life but also by subsequent generations (Jonsson & Jonsson 2014; Gavery & Roberts 2017). Our current understanding of these closed rearing systems is still developing (Good & Davidson 2016; Hines et al. 2019). Investigations are underway to apply this concept towards overcoming problems encountered later in the production cycle such as disease, poor acceptance of alternative aquafeed or malformations in Atlantic salmon and rainbow trout (Geurden et al. 2013; Clarkson et al. 2017; Uren Webster et al. 2018).

However, despite these potential advantages, there are complexities associated with rearing healthy fish in these land-based systems. Crucially, when dealing with adaptations to different environments such as these, there may be a strong genotype by environment interaction (G × E) effect (Sae-Lim et al. 2016). G × E occurs where the performance of the selected animals varies markedly across diverse production environments, which results in re-ranking of genotypes and effectively reduces the overall response to selection within a breeding programme (Sae-Lim et al. 2016). This presents a major issue for aquaculture species’ breeding programmes, which often operate on a global scale. The on-growing of many species occurs under ‘natural’ conditions in ponds or seawater pens, which can be strikingly different from the controlled conditions of breeding nuclei and experimental challenge facilities. Furthermore, technological advances in production settings mean that breeding goals need to be adapted to new production environments, for example RAS, or environments which are likely to be affected by climate change. This may require separate breeding programmes, or targeted breeding for robustness to reduce the G × E effect in these new rearing systems.
History and current status of selective breeding in the UK

The aquaculture industry in the UK is heavily dominated by salmon production, followed by rainbow trout, mussels and oysters. The domestication of these species occurred over very different timescales – the earliest records for blue mussel and Pacific oyster cultivation date from the 13th and 17th centuries respectively (Fujiya 1970; Prou & Goulletquer 2002) whereas rainbow trout and Atlantic salmon cultivation only began in the 19th century (Nash 2011). However, the first scientific reports of breeding each of these species for a specific trait were all published in the 20th century (Lewis 1944; Strömgren & Nielsen 1989; Gjedrem et al. 1991; Kong et al. 2015). Of these, the most advanced selective breeding programmes, and the most advanced genetic tools, are available for the two largest industries—Atlantic salmon and rainbow trout.

Atlantic salmon

The first efforts to collect, incubate and hatch salmon eggs in the UK date from 1838 and were aimed at restocking rivers with wild stocks (Shaw 1840). However, the first salmon farm on-growing fish to harvest did not open until 1969 at Loch Ailort, Inverness-shire. Currently, the vast majority of salmon stock originates from established, large-scale and well-managed breeding programmes with routine trait and pedigree recording. This level of industrial investment in selective breeding research for Atlantic salmon is much greater than any other sector of aquaculture globally and has led to rapid advances in the use of genomic tools such as SNP-chips to improve farmed stocks (Houston & Macqueen 2019). Currently in the UK, key priority traits include resistance to parasitic infection (Amoebic Gill Disease AGD and sea lice), feed efficiency, early maturation and overall stock robustness (Migaud & Houston 2017). Improvements in these traits translate to a rapid gain in commercial production (Gjedrem & Rye 2018). Importantly, disease resistance can also reduce the environmental impacts of chemotherapeutic discharge in the water and pathogen transmission to wild populations (Wargelius 2019).

In 2018, 87% of salmon ova laid down to hatch in Scotland were imported from outside the UK (Munro 2019). UK producers largely source genetically improved eggs from large consolidated pedigree-based selective breeding programmes. Such consolidation of industry research and development activities is necessary due to the high costs. Ova are imported from: AquaGen, based in Norway but with new broodstock facilities opened in Scotland in 2018; Benchmark, based in Norway (Salmobreed) and Iceland (StofnFiskur); and one producer (Mowi) runs its own integrated breeding programme in Norway (Mowi 2019). However, relying on imported stock also has disadvantages. For example, G x E could play a major role in the performance of similar genetic material disseminated to diverse environments. It is well-established in aquaculture species that G × E can be significant for growth and disease resistance traits, and this can cause family re-ranking which reduces the realized impact of genetic gain on commercial production (Sae-Lim et al. 2016). Another disadvantage is the potential risk of importing infectious pathogens, and/or the potential bans on egg imports due to changes in governmental regulations, for example following detection of notifiable pathogens. This has been the case recently for ISAV, which has prevented import of eggs from Norway to the UK since 2019 (Marine Scotland Directorate 2020). This clearly highlights the need to establish UK-based breeding programmes to reduce reliance on Norwegian or Icelandic imports, and to select stocks for improved performance under UK environmental conditions and farming practices. Within the UK, Hendrix Genetics runs breeding programmes (Yáñez et al. 2015) and specialized companies, for example Xelect, provide genetic management services for in-house breeding programmes of some small- to medium-sized UK producers, for example Loch Duart and Wester Ross Salmon (Munro 2019; SAIC 2019b).

UK research and development programmes related to selective breeding and genomics have been underway for several decades, focussed on several economically important traits, including growth, survival, fillet colour and late sexual maturation (reduced grilsing rate) and in particular, disease resistance. Since the 1990s, Norwegian-owned Mowi Scotland (formerly Marine Harvest Scotland) has been involved in genetic improvement programmes aiming at targeting disease resistance traits in farmed stocks in the UK and globally, including sea lice (Jones et al. 2002), AGD (Aslam et al. 2020), cardiomyopathy (Boison et al. 2019) and Pancreas Disease (PD) (Gonen et al. 2015). The first successful documented example of MAS being used for any aquaculture species was the IPN resistance project discussed earlier. This was developed in parallel by UK and Norwegian research groups working with Hendrix Genetics and AquaGen, respectively (Houston et al. 2008; Moen et al. 2009) and was followed by several other collaborative projects between UK and Norwegian academic researchers (Robledo et al. 2016; Ulrich et al. 2018; Rodríguez et al. 2019). It is often the case that breeding research begins via such academic and industry collaborations, before being translated to widespread industry application when it becomes cost-effective. Research projects targeting resistance to the two biggest pathogenic threats to the UK salmon industry at present, sea lice (Tsai et al. 2016; Robledo et al. 2019) and AGD (Robledo et al. 2020) have also successfully produced genome-wide SNP chips suitable for
research (Houston et al. 2014; Lien et al. 2016). Subsequently, several SNP chips have also been developed and widely applied for industry implementation.

Rainbow trout

Since the first 'table trout' farm established in Lincolnshire in 1950, almost 300 rainbow trout farms now exist across the UK, with the majority based in southern England, North Yorkshire and Southern to central Scotland (British Trout Association 2019). Similar to the salmon industry, most of the eggs are sourced from outside the UK, the majority coming from Denmark and Norway, with Northern Ireland contributing 20% of the total UK supply, helping mitigate potential G x E effects (Murphy 2015; Munro 2019). Formerly, stock tended to be all-female, which eliminated male maturation in portion size fish. However, reflecting the trend in the industry for larger marine on-grown fish, most eggs are now triploid which prevents maturation in larger fish. Gender manipulation and induced sterility are important stock management tools in aquaculture which will be discussed later.

Several trout producing companies have invested heavily in UK selective breeding projects. The Seven Springs Trout Hatchery Ltd. in Northern Ireland selectively bred broodstock via a partnership between Dawnfresh Ltd. (a major UK trout farming company) and Hendrix Genetics. This attracted Troutex, a large Danish trout breeding company and ova supplier to purchase a 66% share in the hatchery in 2011 (Troutex ApS 2019). UK producers often source genetically improved eggs through four main external specialized breeding companies, Troutex (based in Denmark), AquaGen (based in Norway), Troutlodge (based in Isle of Man) and AquaSearch (based in Jelling, Denmark). Earlier academic efforts to optimize rainbow trout husbandry in the UK focussed on heritability of stress responses and osmoregulation in the context of stocking density and saltwater tolerance respectively (Pottinger & Carrick 1999; Pottinger & Pickering 2011; Le Bras et al. 2011). In addition to improving growth and feed conversion ratios, breeding programmes have also selected for disease resistance. Successes include increased resistance to *Flavobacterium psychrophilum*, the causative agent of rainbow trout fry syndrome (RTFS) also known as bacterial coldwater disease (BCWD) (Gulla et al. 2016). US-based company Troutlodge was one of the first companies in the world to apply genomic techniques to produce a commercial strain of trout resistant to BCWD (Vallejo et al. 2017; Liu et al. 2018). In the UK, this company is integrated with Hendrix Genetics and continues to use selective breeding to improve survivability, growth, quality, feed conversion rate, meat characteristics and animal welfare. AquaGen is another company heavily invested in selectively breeding trout. In collaboration with UK-based aquaculture companies Cooke Aquaculture Scotland and Dawnfresh Seafoods Ltd., AquaGen are involved in researching the heritability of resistance to diseases such as BCWD in trout (SAIC 2017; Hoare 2018).

*Flavobacterium columnare* is a bacterial pathogen which causes Columnaris Disease or Bacterial Warm Water Disease (BWWD) affecting many aquaculture species besides salmonids, although as the name implies, usually in warmer water. As such, it is not yet a major concern in the UK but could emerge as a disease for UK trout. This disease can cause very high mortality rates and antibiotics are currently the only successful treatment (Declercq et al. 2013). However, efforts to identify resistance markers are underway including a genome-wide analysis (Silva et al. 2018; Silva et al. 2019) which should aid UK efforts to breed resistance. Recent (ARRAINA 2013; FISHBOOST 2014) and ongoing (AquaIMPACT 2019; FutureEU Aqua 2019) European Commission funded projects have been advancing knowledge and developing tools for selective breeding in rainbow trout as well as salmon and other commercially important species in Europe.

Mussel

British growers of mussels, the third most commercially important UK aquaculture species, have long relied on natural settlement of wild spat. Therefore, there has been relatively little demand for hatchery produced seed. Wild sourcing is typically cheaper than hatchery production and is likely to result in genetically diverse stocks negating the risks of inbreeding associated with closed breeding populations. However, this process is susceptible to large temporal and geographical variations in availability, deleterious hybridization with the invasive foolish mussel, climate change and disease. The recent development of species diagnostic SNPs panel (Wilson et al. 2018), potentially linked to QTL affecting important traits such as meat yield and shell strength, has the potential to significantly inform current wild spat collection strategies for establishing base populations and selective breeding trials. A large bivalve hatchery has also been established in the Shetland Islands to mitigate against current and future challenges to wild spat supply, and will be discussed later (Adamson et al. 2018).

Pacific oyster

Two British bivalve hatcheries produce Pacific oyster seed, and unlike hatcheries elsewhere in Europe, both are confirmed as free from all shellfish diseases listed with notification obligations by the OIE or EU (based on their potential social and economic impact) including OsHV-1 and...
protozoan parasites of the Bonamia genus (Adamson et al. 2018). Combined, these hatcheries are the sole supply for all C. gigas seed to UK growers in disease-free areas. However, there would likely be a national seed shortage should conditions change to affect the ability of either hatchery to produce disease-free seed. Substantial research efforts have been made into selective breeding for improved disease resilience and stock husbandry to safeguard against such threats to the UK market (Gutierrez et al., 2018a, 2018b).

Other species

While the four main UK aquaculture species described above represent 98% of production by value, there are several other minor species (Table 2) with important roles and future potential in diversification of production. The UK has recently started producing cleaner fish for sea lice control in the salmon industry (Table 2), which is predicted to increase significantly in coming years to meet demand (Carvalho et al. 2018). Since 2010, several hatcheries have been established throughout the UK by Mowi, Otter Ferry Seafish and Scottish Sea Farms growing both ballan wrasse (Labrus bergylta) and lumpfish (Cyclopterus lumpus). Ongoing research in the UK is looking at QTL analysis of growth and gender with the view to establish marker-assisted selection in the near future. Additionally, their delousing efficacy is also critical and likely to be inheritable and therefore amenable to genetic improvement (Leclercq et al. 2014; Imsland et al. 2016; Brooker et al. 2018).

Atlantic halibut (Hippoglossus hippoglossus) farming began in the UK in 1983 (Baynes et al. 2006) with harvest tonnage peaking in 2005 at 287 tonnes (FAO 2020a). Currently, the UK industry is centred round a single hatchery and associated land based on-growing site with an annual harvest volume of circa 60 tonnes in 2019 (Otterferry Seafish Ltd., Tighnabruaich, Scotland, UK). A long generation time of more than 6 years has hindered the establishment of self-sustaining selective breeding programmes, with relatively few specialized hatcheries worldwide (Puvanendran & Mortensen 2009; Reith et al. 2011). Progress has been made in gender manipulation technology with the first monosex production started in Scotland in 2013 (Palaikostas et al. 2013) and genetic management tools (Reid et al. 2007; Reith et al. 2011).

Atlantic cod (Gadus morhua) farming started in the UK and Norway in the early 21st century driven by reduced wild catches, rising market prices and the potential to use existing salmon farming systems. On-growing production in Shetland peaked at 1822 tonnes in 2008 (Walker 2009), however cod farming collapsed in 2007–2008, partly due to the global financial crisis. While UK operations have not yet restarted, Norwegian family-based selective breeding programmes operated by Nofima have continued, targeting growth, maturation (Kolstad et al. 2006) and disease resistance (Ødegård et al. 2010; Bangera et al. 2011).

The native brown trout (Salmo trutta) has a relatively small aquaculture industry in the UK, with the majority of farms based in England. Most of these are freshwater sites growing for stocking angling waters (Munro 2019). Several grow-out farms for rearing warm-water fish Oreochromis niloticus (Nile tilapia) were established throughout the UK in the past two decades, although none have remained operational. In 2017, however, the first commercial tilapia hatchery in the UK and the second in Europe was established (Fletcher 2017) which attract new UK-based grow-out farming.

The European flat oyster (Ostrea edulis) is the UK’s native edible oyster. As yet, no selective breeding programmes exist, although two hatcheries now commercially

Table 2 Annual UK aquaculture output from hatcheries/nurseries of juveniles reported by number for on-growing, averaged over the period 2013–2018. Excludes juveniles on-grown within the same farm, released for angling/restocking and sold to ornamental fish trade. ‘ nei’ (not elsewhere included) used to combine production of minor species and confidential figures, and groupings differ to Table 1 to preserve anonymity; due to limited number of UK producers, Bivalvia species grouped for confidentiality. Source: Cefas compilation of UK statistics for Eurostat and FAO

| Species & destination for on-grown production | Produced from | UK total (millions per annum) |
|---------------------------------------------|---------------|-------------------------------|
| Finfish – on-grown for consumption, as cleaner fish and for sport angling | Atlantic salmon FW | 49.006 |
|  | Oncorhynchus mykiss FW | 18.050 |
|  | Cyclopterus lumpus SW | 1.720 |
|  | Salmo trutta FW | 0.687 |
|  | Labridae SW | 0.178 |
|  | Osteichthyes FW | 0.002 |
|  | Osteichthyes FW | 0.001 |
|  | Salmonidae FW | 0.125 |
|  | Cyprinus carpio FW | 0.049 |
|  | Osteichthyes FW | 53.606 |
| Shellfish – on-grown for consumption | Bivalvia SW | 53.606 |
produce them, including a single species hatchery recently established in Orkney (Orkney Shellfish Hatchery 2020). While great Atlantic scallop cultivation is practised in the UK, this is entirely reliant on wild spat collection and due to the limited production outputs, there is currently no demand for a domestic hatchery. Although scallops earn a high price on the market, they are slow to grow in British waters and wild stocks are still available, which limits commercial prospects to intensify farming activities. Until recently, all seed production was managed by the Scalpro hatchery in Norway using UK broodstock (Adamson et al. 2018). Scope to increase spat availability and quality and improve growth rate to reduce time to market remain valuable goals in the progression of UK scallop aquaculture.

A small number of warm-water shrimp farms have been established in the UK over many years, for example Pacific whiteleg shrimp (Litopenaeus vannamei) are being grown by Great British Prawns Ltd. in Stirlingshire, Scotland in 2019 using Clearwater RAS technology. This company has established its own hatchery and at full capacity, aims to produce 50 tonnes of L. vannamei per year which should replace some of the UK’s reliance on imported shrimp, mostly from SE Asia (Fletcher 2019). Hatchery techniques for the production of juvenile European lobster (Homarus gammarus) from wild-caught egg-bearing females were pioneered in the UK (Beard et al. 1985). Efforts to improve hatchery conditions for lobster larval rearing have been underway for some time (Hughes et al. 1972; Middlemiss et al. 2015; Small et al. 2015), but several husbandry issues remain. Recent advancements have been made to close the breeding cycle and improve genomic tools available for UK lobster (Jenkins et al. 2019). This should synergize well with efforts to domesticate this species, such as AquaLeap, a major UK academic-industry research project aiming to improve the genetics and breeding for salmon, lobster, flat oyster and lumpfish (SAIC 2019a).

Reports suggest that the UK offers suitable environments for seaweed aquaculture (Capuzzo & McKie 2016), which can provide a source of biofuel production, carbon sequestration and food (Hughes et al. 2012). Although in early stages relative to finish fish aquaculture, the potential for genetic improvement of commercially important traits is well recognized (Robinson et al. 2013). While seaweed cultivation and macroalgae processing industries are not yet established at scale in the UK, this is predicted to change in coming years as technology develops and demand increases, in particular for biofuels (Capuzzo & McKie 2016; Wood et al. 2017).

**Sterility and gender manipulation**

In aquaculture, it is often desirable to produce monosex or sterile stock. Hatchery-reared aquaculture stock are selectively bred for phenotypes suited to farming, which are often not reflective of genotypes found in the wild. Many view this as a significant concern for the open-culture systems used in all major sectors of UK aquaculture due to the potential for escapes to negatively impact on wild populations (Glover et al. 2017). In particular for wild freshwater and anadromous fish such as salmon with relatively small effective population sizes, gene pools found in nature can be significantly affected by influx of genes from farmed animals (Hindar et al. 2006; Glover et al. 2017). Conversely, it has been suggested that interbreeding with captive native oyster stock may benefit sparse wild populations by contributing to genetic variation (Varney et al. 2018; Hornick & Plough 2019). Besides preventing introgression effects of escapes from farms, sterility can also avoid early maturation during on-growing, which may negatively affect growth, welfare and product quality leading to harvest downgrades. Importantly, sterility can also be used to protect intellectual property (IP) generated from long-term improvement programmes run by breeding companies.

The triploid methodology was first implemented in the rainbow trout industry in the 1980’s and has since been adopted by farmers all over Europe, including the UK (Munro 2019), in conjunction with monosex female (discussed below). Triploidy is induced by exposing the fertilized eggs to hydrostatic pressure or temperature shock. All female offspring are produced by fertilizing normal female eggs with milt from masculinized genetic females (Dunham & Plough 2019). Besides preventing introgression effects of escapes from farms, sterility can also avoid early maturation during on-growing, which may negatively affect growth, welfare and product quality leading to harvest downgrades. Importantly, sterility can also be used to protect intellectual property (IP) generated from long-term improvement programmes run by breeding companies.

Despite the widespread use of induced sterility in UK trout, it has yet to be similarly adopted for UK salmon farming (Leclercq et al. 2010; Gabian et al. 2019). Although the UK has been at the forefront of salmonid sterility research from the 1970s (Johnstone et al. 1979; Lincoln & Scott 1983; Bye & Lincoln 1986) and more recently over the last twelve years with Stirling led Salmotrip projects funded by EU, BBSRC and industry (Taylor et al. 2007; Taylor et al. 2013; Taylor et al. 2015), sterile triploid Atlantic salmon are mainly supplied to Norwegian salmon producers by most breeders (Aquagen, Salmobreed, StofnFiskur). This follows the launch of green licences in 2013 (Hersoug 2015) to tackle demonstrated impacts of farmed salmon escapes in Norwegian rivers (Glover et al. 2017). Over recent years, knowledge of triploid salmon physiology has progressed vastly, leading to recommendations and protocols to address challenges faced by the...
industry, for example suboptimal growth and welfare, reduced robustness, environmental sensitivity and nutritional requirements (Taylor et al. 2013; Taylor et al. 2015). However, a basic understanding of triploid salmon genetics is still lacking, and the genetic correlation between target traits for breeding observed in conventional diploids and in triploids is not well known. As such, tailored breeding programmes may be required to support routine triploid production.

Besides induced sterility or triploidy, it may also be desirable to control the age of sexual maturation. The gene vgll3 has been discovered to explain 30–40% of phenotypic variation in maturation age (Verta et al. 2020). A technology which could radically progress these efforts in fish is the direct disruption of genes involved in germ cell development through gene editing (Güräl et al. 2020), which will be discussed later.

Alongside induced sterility, gender manipulation is routinely performed in several commercially important finfish species, including rainbow trout (monosex female), tilapia (monosex male) and more recently monosex female in halibut (Palaikostas et al. 2013). Many aquaculture fish species exhibit strong sexual dimorphism for a number of commercially relevant traits such a growth and age of maturity (Leclercq et al. 2010). This has led to interest in understanding sex determination and methods to control it. For instance, male tilapia display 40% faster growth rates and higher FCR than females (Mair & Abella 1997; Beardmore et al. 2001). Following an eight year breeding study within the UK Department for International Development (formerly ODA) Fish Genetics Research Programme at Swansea University, Wales (Scott et al. 1989), a genetically unique form of Supermale tilapia was developed with a YY genotype rather than the usual XY. The result is all-male offspring without the use of chemical or hormonal treatment. This strain is known as Genetically Male Tilapia (GMT), which are produced by the Three-Sixty Aquaculture hatchery in Swansea (Fletcher 2017). This avoids direct hormonal sex reversal using 17α-Methylidihydrotestosterone (MDHT), widely practised globally but banned in the European Union (Directive 1996).

Concern surrounds the effects of non-native Pacific oyster settlement on UK ecosystems (Herbert et al. 2016). This is a significant reason to farm sterile stock, and the only commercially available method is to generate triploid animals. Although heat and chemical shocks can be used to induce triploidy, a common method involves crossing a diploid animal with a fully fertile tetraploid parent, resulting in a triploid individual. As such, any selective breeding programme harnessing triploids would have to consider the performance as triploids and maintain both tetraploid and diploid breeding animals. Triploid oysters are also considered desirable for aquaculture, because more of their energy is directed towards growth instead of reproduction. This avoids the unfavourable ‘milkeness’ which otherwise occurs during the summer spawning period, allowing triploids to be sold year-round. Additionally, use of sterile stock allows farms to establish more easily in new areas (Adamson et al. 2018). Triploid Pacific oysters are available to UK farmers but are not always used due to the higher cost of seed.

Triploid induction in blue mussels seeds has been investigated (Kamermans et al. 2013). However, because mussels are usually consumed cooked, poorer meat quality during the spawning season is less of an issue than for oysters. Indeed, mussels are harvested year round, and the gonad development preceding spawning contributes to the meat yield and product quality. It will be important to evaluate whether triploidy could produce adequate and more stable meat yields by potentially reducing post-spawning weight loss. Sterility induced by triploidization is to be expected in mussels but has not yet been demonstrated. As discussed earlier, mussel aquaculture in the UK has been negatively affected by the introgression of M. trossolus with the native M. edulis resulting in softer shells and lower meat yields (Michalek et al. 2016). While hatchery-produced spat could ensure native M. edulis are cultivated, introgression of hatchery-produced spat genetics may have a negative effect on the wild populations of blue mussel, as suggested for in Atlantic salmon (Glover et al. 2017). While selective breeding from local stocks reduces this concern, directional selection in a closed breeding programme will result in cumulative divergence between the improved and wild strains, and the issue will therefore remain.

Current breeding technology innovations and future applications

With the advancement of aquaculture industries, the tools and resources routinely used in Atlantic salmon breeding and cultivation are becoming adopted by other finfish sectors and increasingly by shellfish farmers. The current status, and likely next steps for breeding technologies applied domestically and globally to each of the four main UK aquaculture sectors is summarized in Table 3. Some of the innovations and developments which are likely to be adopted in coming years are discussed below.

Genomic selection requires a platform to generate high-density SNP marker genotypes across populations of animals. For example, previous studies of genomic selection in Atlantic salmon have typically used sample sizes of 500–3000 individuals (Odégard & Meuwissen 2014; Tsai et al. 2015; Yanez et al. 2015; Tsai et al. 2016; Robledo et al. 2019; Rodriguez et al. 2019) which can be prohibitively expensive. Fortunately, the cost of genotyping an animal reduces markedly with scale, and recent studies have
Table 3: Current level of breeding technologies applied to each of the four main aquaculture species in the UK and globally. In addition to *Mytilus* spp., ‘Mussel’ includes all *Mytilid* mussel species grown globally, for example *Perna canaliculus* (New Zealand green-lipped mussel).

| Breeding technology | Application | UK | Global |
|---------------------|-------------|----|--------|
| **Atlantic Salmon** |             |    |        |
| Closed breeding cycle | Commercial |    |        |
| Mass selection | Commercial(Domestic stock) |    |        |
| Family selection | Commercial |    |        |
| Sib testing/selection | Commercial |    |        |
| Gender manipulation/triploidy | Academic |    |        |
| Marker-assisted selection (MAS) | Commercial |    |        |
| Genomic selection (GS) | Commercial |    |        |
| Genome editing (GE) | Academic |    |        |
| Gene-edited organism (GEO) | Academic |    |        |
| **Rainbow Trout** |             |    |        |
| Closed breeding cycle | Commercial |    |        |
| Mass selection | Commercial |    |        |
| Family selection | Commercial |    |        |
| Sib testing/selection | Commercial |    |        |
| Gender manipulation/triploidy | Academic |    |        |
| Marker-assisted selection (MAS) | Commercial |    |        |
| Genomic selection (GS) | Commercial |    |        |
| Genome editing (GE) | Academic |    |        |
| Gene-edited organism (GEO) | Academic |    |        |
| **Mussel** |             |    |        |
| Closed breeding cycle | Commercial |    |        |
| Mass selection | Commercial |    |        |
| Family selection | Commercial |    |        |
| Sib testing/selection | Commercial |    |        |
| Gender manipulation/triploidy | Academic |    |        |
| Marker-assisted selection (MAS) | Commercial |    |        |
| Genomic selection (GS) | Commercial |    |        |
| Genome editing (GE) | Academic |    |        |
| Gene-edited organism (GEO) | Academic |    |        |
| **Pacific Oyster** |             |    |        |
| Closed breeding cycle | Commercial |    |        |
| Mass selection | Commercial |    |        |
| Family selection | Commercial |    |        |
| Sib testing/selection | Commercial |    |        |
| Gender manipulation/triploidy | Academic |    |        |
| Marker-assisted selection (MAS) | Commercial |    |        |
| Genomic selection (GS) | Commercial |    |        |
| Genome editing (GE) | Academic |    |        |
| Gene-edited organism (GEO) | Academic |    |        |
suggested that low-density SNP panels are sufficient to achieve accurate genomic predictions (Kria里ou et al. 2020), with genotype imputation offering further avenues to improve cost-efficiency. (Tsai et al. 2017; Tsairidou et al. 2020). One constraint is that low-density SNP panels are effective when the training and test populations are closely related (e.g. within a year group of a breeding programme), but predicting breeding value of more distantly related animals is often inadequate (Meuwissen et al. 2014; Tsai et al. 2016). This may be resolved by the detection and use of functional variants impacting the trait directly, rather than linked markers, and is becoming more achievable via the routine use of modern genomics, sequencing and genome editing technologies (Houston et al. 2020). High-quality reference genome assemblies are important in genomic assisted breeding and use of genomic tools. The available genome assemblies of current and potential future UK aquaculture species are presented in Table 4. While no reference genome assembly has been published yet for blue mussels, there is a mitochondrial genome and a microsatellite linkage map of 791 markers (Boore et al. 2004; Lallias et al. 2007). Reference genomes for the closely related Mediterranean (M. galloprovincialis) and Korean (M. coruscus) mussel has been published (Table 4) and will help in assembling the blue mussel genome. Assemblies are also lacking for the native oyster (Ostrea edulis), queen scallop (Aequipecten opercularis) and European abalone (Haliotis tuberculata); although many of these are currently in progress. Assembling a genome is not a trivial task, and many are complicated by the high levels of genomic sequence variation, heterozygosity (sequence variation between chromosome pairs), repetitive sequences of DNA and whole genome duplication events which are common in several aquaculture species (Berthelot et al. 2014; Lien et al. 2016; Hollenbeck & Johnston 2018).

State of the art in breeding and genomics of finfish

The adoption and pace of technical innovations in genomics and selective breeding is realized quicker in salmonid species farmed in the UK by large multinational industries who are able to allocate the required budgets. At the moment, genomic selection is the state of the art for salmon breeding (Table 3). Marker-assisted selection and genome-wide marker SNP array platforms have been used to improve salmon stock across several phenotypes (Zenger et al. 2018) including disease resistance (Gonen et al. 2015; Robledo et al. 2016; Robledo et al. 2019; Silva et al. 2019; Rodriguez et al. 2019; Robledo et al. 2020), body size and weight (Reid et al. 2005; Baranski et al. 2010; Gutierrez et al. 2012; Tsai et al. 2015), but also delaying sexual maturation which can improve growth and meat quality (Pedersen et al. 2013; Gutierrez et al. 2014; Ayillon et al. 2015; Barson et al. 2015). As domestication of farmed Atlantic salmon progresses, genomic tools may also be used to assess impacts of the domestication process, examining the genetic basis for changes in growth, morphology, behaviour and physiology (Glover et al. 2017; López et al. 2019).

Understanding how a genotype gives rise to an observable phenotype is a major challenge. Closing the genotype to phenotype gap relies initially upon a broad understanding of the variants across a genome which affect a given trait. This depends heavily on accurately measuring and recording detailed trait information for large numbers of individual animals. Due to the nature of their husbandry and number of animals kept, such large-scale trait recording for aquaculture species presents unique challenges. A clear goal for future development should be to improve the range, accuracy and automation of collecting trait measurements on the animals (phenotyping). Major initiatives for functional annotation, that is assigning biological information to regions of a genome sequence, are underway in livestock (Functional Annotation of Animal Genomes (FAANG)) (Andersson et al. 2015; Giuffra et al. 2019), and more recently for salmonid species including Atlantic salmon and rainbow trout (Macqueen et al. 2017). The ambitious efforts of these large projects should prove very useful in improving the application of genomics to UK salmon and trout breeding and production. Outputs from these programmes will also synergize with advances in genome editing tools. Genome editing (discussed below) can be used in laboratory experiments to increase our understanding of salmonid biology, or potentially directly to improve salmonid broodstock in the future.

Assays and computing for such functional annotation is expensive and requires strategic and often international investment. For emerging or new aquaculture species in an earlier state of domestication, sequencing, assembly and more basic sequence annotation should be an initial priority. A good example of these technologies being successfully used to rapidly fast-track domestication of new aquaculture species is that of ballan wrasse and lumpfish for deployment as cleaner fish, the production of which is becoming a major sector in UK aquaculture (Carvalho et al. 2018; Brooker et al. 2018). The commercial cultivation of ballan wrasse began in the UK in 2010 with the joint venture between Mowi (former Marine Harvest) and Scottish Sea Farms in Machrihanish (Scotland) followed by lumpsucker in 2013 by Ocean Matters in Anglesey, Wales, now also owned by Mowi (Treasurer 2018). Advanced breeding technologies (e.g. gamete assessment, fecundity estimates) led to closing the life cycles of both species (Treasurer 2018; Pountney et al. 2020), and reference genomes released to the public domain by 2018 (Treasurer 2018; Lie et al. 2018; Knutsen et al. 2019). Using these resources, the
development of SNP-based toolkits for commercial breeding programmes is currently underway. This is an excellent demonstration of what can be achieved using these multifaceted modern technologies.

**State of the art in breeding and genomics of shellfish**

Bivalve genetics differ from those of finfish in several ways due to biological phenomena which are well explained in a recent review (Hollenbeck & Johnston 2018). Very high levels of heterozygosity with marked segregation distortion (e.g. higher genotypic frequency than expected) and high levels of polymorphism, even with close/consanguineous breeding, contribute to computational difficulties in assembling a reference genome (Houston et al. 2020). However, these exact phenomena, and very high fecundity, allow bivalves to maintain a high genetic diversity despite intense selection in the wild. For example, studies have shown that bivalves carry high genetic loads (i.e. high levels of genetic mutations, often deleterious), which are expressed differently against various selection backgrounds (Plough 2016; Plough et al. 2016). For these reasons, the ratio of within-family to between-family variation is likely to be considerably higher in bivalves than finfish, suggesting that capturing this variation via genomic selection would provide relatively larger gains than in most species. In family-based and mass selection studies across several mollusc species, the average response to selection per generation across all taxa for growth was 10.6%, while selection for disease resistance traits was 15.7% (Hollenbeck & Johnston 2018).

### Table 4 Genome assemblies for UK aquaculture industry relevant species

| Species                          | Total size (Mb) | Contig N50 (Kb) | Scaffold N50 (Mb) | Sequencing platform | Reference                                      |
|----------------------------------|----------------|-----------------|------------------|---------------------|------------------------------------------------|
| Atlantic salmon (Salmo salar)    | 2967           | 57.6            | 1.366            | Illumina HiSeq; PacBio; Sanger; Illumina GAIIx  | GenBank: GCA_000233375.4 (Lien et al. 2016)   |
| Rainbow trout (Oncorhynchus mykiss) | 2333           | 16 039          | 85.33            | PacBio Sequel       | GenBank: GCA_013265735.1                       |
| Pacific oyster (Crassostrea gigas) | 648            | 1564            | 58.46            | PacBio              | GenBank: GCA_902806645.1                       |
| Mediterranean mussel (Mytilus galloprovincialis) | 1500          | 2.63            | 0.29             | Illumina HiSeq      | GenBank: GCA_001676915.1                       |
| Korean mussel (Mytilus coruscus)  | 1904           | 817             | 898              | Illumina HiSeq; PromethION | GenBank: GCA_011752425.1 (Li et al. 2020b)    |
| Ballan wrasse (Labrus bergylta)  | 805            | 703.9           | 0.80             | Illumina HiSeq; PacBio        | GenBank: GCA_900080235.1                       |
| Lumpfish (Cyclopterus lumpus)    | 573            | 4950.1          | 23.90            | Illumina HiSeq; PacBio     | GenBank: GCA_009769545.1                       |
| Sea/brown trout (Salmotrunta)   | 2372           | 1703            | 52.21            | PacBio; Hi-C; 10X Genomics Chromium; BioNano  | GenBank: GCA_901001165.1                       |
| Great Atlantic scallop (Pecten maximus) | 918           | 1258.4          | 44.82            | PacBio; Hi-C; 10X Genomics Chromium      | GenBank: GCA_902652985.1                       |
| Nile tilapia (Oreochromis niloticus) | 1006           | 2923.6          | 38.84            | PacBio              | GenBank: GCA_001858045.3                       |
| Common carp (Cyprinus carpio)    | 1714           | 75.1            | 7.83             | Roche 454, SOLiD, Sanger BAC-end | GenBank: GCA_000951615.2 (Xu et al. 2014)     |
| Turbot (Scophthalmus maximus)    | 557            | 20 466          | 25.95            | PromethION          | GenBank: GCA_013347765.1                       |
| Atlantic cod (Gadus morhua)      | 670            | 1015.7          | 28.73            | PacBio              | GenBank: GCA_902167405.1                       |
| Pacific white shrimp (Lipotenaerus vannamei) | 1663         | 86.86           | 0.61             | PacBio, Illumina HiSeq | GenBank: GCA_003789085.1                       |
| Atlantic halibut (Hippoglossus hippoglossus) | 597          | 7020.3          | 26.31            | PacBio; Illumina NovaSeq; Hi-C; DLS       | GenBank: GCA_009819705.1                       |
| European sea bass (Dicentrarcus labrax) | 676           | 54.13           | 26.44            | ABI 3730xl; ROCHE 454 FLX Titanium; Illumina GAIIx | GenBank: GCA_000689215.1 (Tine et al. 2014)   |
| Arctic charr (Salvelinus alpinus) | 2170           | 55.6            | 1.02             | Illumina Paired-End; Illumina Mate-Pair; PacBio | GenBank: GCA_002910315.2 (Christensen et al. 2018) |

†Contigs are contiguous stretches of sequenced bases (A, C, G or T) without any gaps.
‡The N50 is measure of the quality of genome assembly contiguity. It is a weighted median statistic where 50% of the entire assembly is covered by contigs/scaffolds equal to or longer than this value.
§Scaffolds are made by joining contigs together based on information about the orientation and position of a contig in a genome.
non-existent (Gutiérrez et al. 2017) through to homozygous or more typically heterozygous deficiencies (Beaumont 2008; Hedgcock et al. 2015). However, higher selection intensity could potentially be performed without risking deleterious consequences of inbreeding (Hornick & Plough 2019; Houston et al. 2020). To achieve this, understanding the impact of targeted crossing and hatchery culture on long-term population genetic characteristics will be important for well-managed breeding programmes using genomic selection.

For selective breeding in Mytilid mussels, New Zealand aquaculture is arguably leading the way; a government funded Primary Growth Partnership programme has enabled commercial production of Greenshell™ Mussel spat (Perna canaliculus). Unlike an industry with wild spat dependence, this move has allowed for generational genetic improvement, and maintenance of pedigree lines (Paredes et al. 2012; Adams et al. 2015; Rusk et al. 2020). Using family selection, the programme aims to supply 30% of New Zealand’s production (Symonds et al. 2019). In this way, their industry can be safeguarded and future-proofed from perturbations affecting wild spat supply, such as emerging diseases and climate change.

To mitigate against increasing variations in wild spat supply (Avdelas et al. 2020), a pilot scale commercial mussel hatchery was established in the Shetland Islands with the ambition to buffer the industry’s reliance on wild resources (Hambrey & Evans 2016; Adamson et al. 2018). An aim of the Shetland hatchery project is to develop SNP-based stock management tools for M. edulis and the establishment of a family selection programme. This move could prove to be greatly beneficial in securing the future of the UK’s largest shellfish aquaculture sector. Simple traits to target in early domestication include increased quality of gametes, survival and resilience of the progeny (Brooker et al. 2018). Closing the breeding cycle in a robust and reproducible way is the first step to using mass selection with management of genetic diversity, or ultimately family selection for commercially relevant traits such as disease resistance, growth, meat yield and shell strength (Table 3).

The past attempts and successes of industrial and experimental selective breeding programmes for oysters worldwide are well covered in other reviews (Hollenbeck & Johnston 2018; Tan et al. 2020). Many of these programmes relied on mass (individual) selection, with some relying on family selection, and some combining the two. Although mass selection has less control for inbreeding, results from these programmes are encouraging, particularly for resistance to diseases threatening UK oyster cultivation – OsHV-1 (C. gigas) and bonamiosis (Ostrea edulis) (Lallias et al. 2008; Dégremont 2011; Camara & Symonds 2014; Symonds et al. 2019; Vera et al. 2019). As better reference assemblies become available (Table 4), it will be possible to produce more improved high-density SNP arrays (Qi et al. 2017; Gutiérrez et al. 2018a), or more affordable tools such as Genotyping-in-Thousands by sequencing (GT-seq) (Campbell et al. 2015). This enables high-throughput genotyping, making genomic tools more affordable and accessible to future UK oyster hatchery management, ideally incorporating family selection and maintaining pedigree lines (Table 3).

**Genetic engineering**

In 1989, AquAdvantage salmon was created by AquaBounty. It is a genetically modified (GM) transgenic Atlantic salmon with a growth hormone regulator from Chinook salmon inserted under a promoter sequence from ocean pout. This enabled year-round growth free from seasonal restriction, and the insert was found to be stable across generations (Yaskowiak et al. 2006; Ignatz et al. 2020). It was the first GM animal approved for human consumption in the USA and Canada (Waltz 2017). However, GM animals are not currently approved for human consumption in the UK, or favourable to the UK consumer market (Mehmet 2020). For now, selective breeding remains the preferred and accepted method of genetic improvement of stocks for aquaculture production. However, the increasing availability and accessibility of genome editing tools, with demonstrated success in whole animals for producing disease resistance (Proudfoot et al. 2019), may lead to genetic engineering tools becoming more commonplace in providing solutions to problems in food security in general (Godfray et al. 2010). Provided appropriate management of GM animals, such as sterility and the use of land-based facilities to avoid escape and introgression, these technologies could greatly benefit aquaculture.

Advancement of genome editing tools, such as CRISPR/Cas9, has arguably the greatest potential to revolutionize livestock and aquaculture breeding at present. This disruptive technology allows researchers to perform functional studies on genomes of a very diverse range of organisms by knocking out (deleting), or upregulating (increasing activity of) genes, in addition to inserting, deleting or even epigenetically manipulating regions of DNA (Knott & Doudna 2018). It has already been used experimentally to induce sterility in several aquaculture species. This can involve disrupting genes involved in sexual maturity, as seen in the Peruvian scallop, Argopecten purpuratus (Thresher et al. 2014), or ablation of germ cells by knocking out the dnd gene in Atlantic salmon (Wargelius et al. 2016; Güralp et al. 2020) or piwi2 gene in Nile tilapia (Jin et al. 2020). These demonstrations of gene editing technology to control sterility open the door to targeting many other desirable traits. It facilitates testing and identification of variants in aquaculture genomes which directly affect economically
important traits, such as precise identification of the causative SNPs in a QTL region (Gratacap et al. 2019; Gratacap et al. 2020a). The use of whole organism (in vivo) editing to generate genetically modified organisms can rapidly accelerate domestication programs, or eliminate disease susceptibility in a precise and targeted fashion (Proudfoot et al. 2019). An exciting prospect is that genome editing in aquaculture species offers several advantages over other livestock groups. Due to the typically high fecundity and external fertilization, access to thousands of embryos at relatively low cost is achievable. This, coupled with the fact that aquaculture species are in a very early stage of domestication, could lead to incredibly rapid progress in coming decades. However, further studies should focus on reducing negative effects such as incomplete editing across every cell in the organism (mosaicism) when using CRISPR/Cas9 to facilitate direct functional analysis (Jin et al. 2020). This can occur when editing takes place at any stage of development beyond embryo and can lead to failure of the desired phenotype being exhibited, or passed on to the next generation.

Beyond creating GMOs, the ability to edit the genome of any study organism allows us to study the effects of individual genetic markers, genes and even SNPs on phenotypic traits (Wargelius et al. 2016; Wargelius 2019). The identification of causative SNPs can increase the accuracy of marker-assisted breeding and retain broodstock genetic diversity when selecting for specific traits such as disease resistance. Using reverse genetic screening (studying the effect of gene deletion), we can gain an increased understanding of gene function for a desired phenotype in a rapid and high-throughput manner (Doench 2018; Gratacap et al. 2020b). Every step required for these CRISPR screens has now been achieved in salmon cells in vitro, including efficient lentiviral vector delivery and antibiotic selection of transduced cells (Gratacap et al. 2020b). This important result demonstrates the ability to perform genome-scale CRISPR screens (Hanna & Doench 2020; Li et al. 2020a) in salmon.

However, this technology is in a relatively formative stage. Genome editing methods must first be refined to ensure robust and repeatable results. Appropriate agreement with industry stakeholders and the general public on what risks and benefits genome editing entails is essential when considering public and regulatory acceptance of the technology for a production setting. Currently, genome editing in the UK is regulated through a combination of EU and domestic legislation, while regulatory provisions across the world remain varied. Authorization is required by European Regulation (EC) No 1829/2003 to use food or feed containing or consisting of GMOs, and food or feed produced from or containing ingredients produced from GMOs, as required. Once the European Food Safety Authority (EFSA) panel has finished its assessment, the European Commission and Member States decide whether to grant authorization of the GMO for use in Europe (Brader 2020). The outcome of a case ruling in 2018 (ECJ 2018) meant that the European Court of Justice (ECJ) does not differentiate between gene-edited organisms (GEOs) and transgenic organisms in all respects, including GEOs which are otherwise indistinguishable from organisms bred by conventional means (Wasmer 2019). However, following requests from Members of European Parliament (MEPs) to revise regulation on GEOs, the EU Council requested the Commission (Council Decision (EU) 2019/1904) to submit ‘a study in light of the Court of Justice’s judgement in Case C-528/16 (ECJ 2018) regarding the status of novel genomic techniques under Union law’ (i.e. Directive 2001/18/EC, Regulation (EC) 1829/2003, Regulation (EC) 1830/2003 and Directive 2009/41/EC) in November 2019. This study will take into account an analysis of the ethical and societal implications of gene editing that is being developed by the European Group on Ethics in Science and New Technologies. The outcome of this report is expected to be published by April 2021 and could have enormous impact on future legislation surrounding GEO and GMOs used in European agriculture. The final regulatory position for genome editing in the UK post-Brexit remains to be seen (Brader 2020).

Conclusion

For the foreseeable future, Atlantic salmon will continue to be the main UK aquaculture species and largest farmed food export. Continued research and development investment by large companies should allow UK salmon farming to keep pace with the integration of latest breeding technologies as production increases. This will include advances in genomic selection to expedite the development of stocks to address key challenges facing the industry; that is, increased robustness and resilience in changing environments (RAS, climate), disease resistance and adaptation of fish to increasingly vegetarian diets. Genome editing is perhaps the next frontier for salmon breeding, and co-investment in research to develop this technology between industry and public funding will facilitate its development. Innovations to tackle key sustainability and environmental concerns (e.g. biological (cleaner fish) control of parasites, reproductive containment (sterility), nutritional imprinting) will drive the salmon farming expansion, whereas trout production is predicted to remain steady in the near future, with reductions in freshwater farming being offset by increased seawater farming (Carvalho et al. 2018). While selective breeding in salmonids has received heavy investment globally, domestic selection programmes for both salmon and trout in the UK will reduce reliance on imported stocks and tackle potential G x E effects.
For the shellfish sector, reduction in wild-spat availability may lead to a further decline in UK mussel production unless offset by offshore mussel farming, and investment in hatchery and breeding technology is critical. Pacific oyster production will likely continue its strong upward trajectory, while native European flat oyster production has been declining since 2008 (Carvalho et al. 2018; FAO 2020a). However, increased interest in hatchery production of European flat oyster seed to support restoration efforts may reverse this decline (Pogoda et al. 2019). Further government investment into innovation in tailored stock management and breeding technologies is required to ensure the sustainability of these industries. Consolidation of smaller businesses to develop larger shellfish industries through farmer associations and cooperatives would potentially allow adoption of commercial selective breeding practices for hatchery-produced seed, currently restricted by the scale of investment required. The implementation of well-managed breeding programmes can avoid some of the issues with fragmented broodstock populations susceptible to inbreeding depression and problems with disease and competition. For these reasons, the development of disciplined breeding programmes for major aquaculture species should be a research and development priority in shellfish (You & Hedgcock 2019).

The UK is very well placed in terms of its academic, technological and marine resources, in addition to strong local and export markets, to expand established and develop new aquaculture species sectors. As yet, it is unclear how potential changes in post-Brexit trade agreements will affect domestic and export markets for UK aquaculture products. Improved hatchery and culture capabilities, together with investment in routine trait measurement, genetic resource management and genomic tools can all contribute to the sustainability and expansion of the UK Aquaculture sector. This can be helped by consolidation and/or integration of smaller sectors, which could then afford investment in development and application of genetic technology and innovations. Local breeding, and/or phenotyping, programmes based in the UK should also be developed alongside multinational breeding programmes. These efforts will help certification as UK origin and branding, avoid supply risks associated with disease status of imported stocks from foreign hatcheries and potentially help tackle G x E interactions. The prominence of UK aquaculture within Europe is due to the high quality product delivered from well-managed integrated salmon breeding programmes using advanced breeding technologies. In a global market, it is crucial that these modern tools and technologies are embraced and developed to maintain this status for salmon farming, and to realize the potential for other aquaculture species into the future.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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