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Science of Salmon Stocking: Scientific Considerations in Stocking Policy Development for River Managers

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Science of Salmon Stocking: Scientific Considerations in Stocking Policy Development for River Managers

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Executive summary

Atlantic salmon is an iconic species of significant cultural and economic importance in countries around the N. Atlantic Ocean basin. The species has been in long term decline and is becoming locally extinct or in poor conservation status across a growing sector of its historic range. The need to respond has focussed attention on the contentious management option of stocking populations with reared fish, which has been deployed in various contexts for over a century. This overview seeks to bring together the science behind the various considerations needed to be taken prior to and following stocking, with a view to aiding design of salmon management strategies that balance risks and benefits within a broad policy framework. Benefits are generally categorised within contexts of conservation and enhancement of salmon populations, and as mitigation for imposed pressures. Risks are generally categorised as potential genetic and ecological damage to populations, including transfer of parasites and pathogens. Supplementation of wild populations with salmon raised in hatcheries can play a part in securing benefits, but may also have potential to cause significant and long-lasting harm, depending on the situation. Understanding the available science is required by stakeholders constructing management plans, by policy makers setting the broad context for using stocking and by regulators assessing proposals. Development, assessment and application of stocking plans should follow a series of procedures to 1) consider whether stocking is required; 2) consider non-biological, ecological, general hatchery, implementation and operational factors; 3) consider detailed hatchery and broodstock issues; 4) evaluate fish release options; 5) consider monitoring strategies; 6) apply review and feedback as adaptive management. Here we review application of the available science for informing these processes.

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1. Introduction

Atlantic salmon (*Salmo salar*) are spawned in rivers and develop in freshwater for a number of years before undergoing a marine feeding migration of up to many 100s of km's with eventual return to natal spawning grounds after one or more years to reproduce. Some males spawn in freshwater without first migrating to sea, whereas in most populations all females are anadromous. Thus, populations of salmon are vulnerable to poor environmental conditions across a broad area of marine and freshwater environments. The Atlantic salmon is a cultural and conservation icon. It is also the subject of commercial net and recreational sport fisheries in many countries around the North Atlantic Ocean basin. For centuries, salmon populations have suffered pressures due to human use of river habitats, for example, suffering from pollution, abstraction of water and obstruction to migration. In recent decades, as many river conditions have been improved, the significant declines in populations seen throughout the range (Friedland *et al.*, 2009; Chaput, 2012; ICES, 2019) appear to be associated with changes in marine conditions (Chaput, 2012; Olmos *et al.*, 2019). For more than a century, stocking has been undertaken to try to increase production and offset such declines (Molony *et al.*, 2003).

Stocking has been utilised in a wide variety of applications which are examined in detail below. However such interventions have been associated with significant controversies (Waples, 1999) and there has been much debate as to the effectiveness of stocking (Waples, 1999; Naish *et al.*, 2007; Araki and Schmid, 2010) due to significant risks involved (Young, 2017). Under different jurisdictions and in differing circumstances, regulatory authorities have decided on different approaches, ranging from case-by-case justification to outright bans of stocking (reviewed in Chaput *et al.*, 2017). Restrictions, and closures of stocking programmes (Harrison *et al.*, 2019a), have been associated with conflict between stakeholder groups (Harrison *et al.*, 2019b). Hence, it is fundamentally important that there is clarity regarding the reasoning behind decision making and the strength of available evidence.

The suitability of stocking as a management tool is governed by two cost-benefit considerations. Firstly, financial: does the cost of investing in stocked fish result in a nett benefit to income and/or capital value of a fishery? Secondly, environmental: does the financial or potential conservation benefit of stocking justify the associated biological risk? The first of these assessments is primarily a matter of business judgement that can be informed by scientific understanding of the biology of salmon. The second question is of more general interest because in this case the risks of stocking have potential to cause damage to populations that are a national resource of immense value. It is not a simple process to evaluate these risks and benefits, particularly because the scientific understanding is incomplete. In many countries Governmental regulation is applied to this risk assessment with the aim of safeguarding salmon as a national resource and in fulfilling legal conservation responsibilities. However, this is not always the case. For example, in Scotland, powers rest with devolved local fisheries management Boards comprised of owners of fisheries, where such Boards exist.

The first part of this review identifies various benefits of stocking and reviews evidence for associated risks that should be considered. Then, the review identifies decision hierarchies that can be followed by fisheries managers and regulatory bodies, considers relevant scientific understanding and defines uncertainties. It is intended that the overview will provide a useful decision-making tool for informed managers and policy developers. Although the focus is on Atlantic salmon, the review refers to salmonid fishes more widely and, as such, draws lessons from, and has relevance to, a wide range of stocking efforts underway or in development.

2. Management objectives and potential benefits

In general, the intended benefit of a stocking programme is to increase numbers of salmon compared with taking no action. This simple objective covers situations ranging from replacing a population that has become extinct to increasing yield of an already productive fishery. In some cases, such as when salmon are reared to the smolt stage and then released (*ranching*), increasing numbers may be for the short-term benefit of a fishery harvesting the stocked fish irrespective of potential longer-term damage to the population. However, in most cases, fisheries managers are concerned with ensuring sustained increase in numbers of salmon within a population. The conservation potential, socioeconomic consequences and risks vary across the range of types of wild supplementation situations. A starting point for managers is to clarify intended benefits.

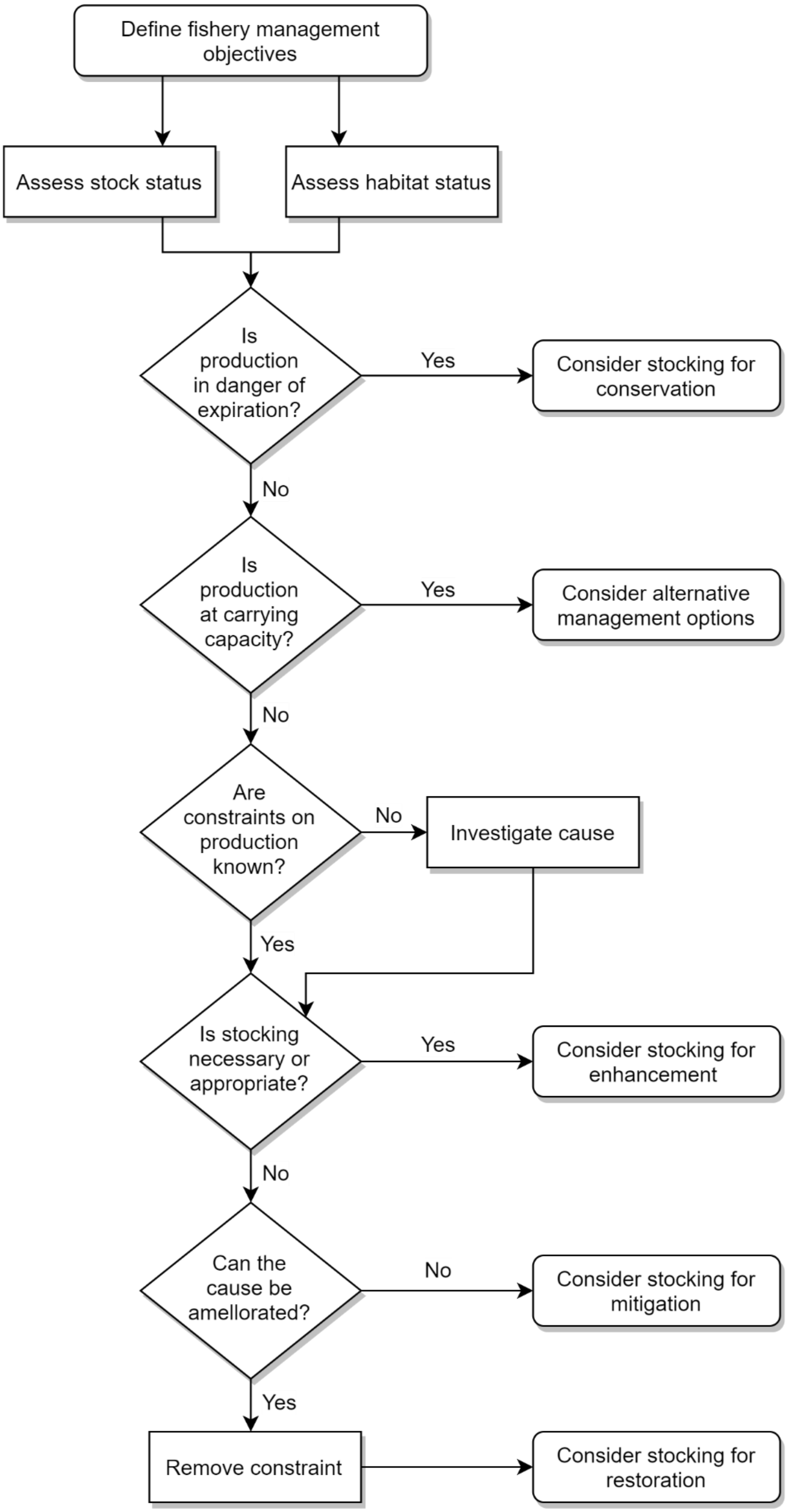

Figure 1 Steps in the development of a successful stocking programme (redrawn after Cowx, 1994b).

Consideration of stocking as a management tool, and the eventual success of this approach, depends on an evaluation of the objectives for initiating the intervention following the process in Fig. 1. Such objectives fall into four broad categories: conservation, mitigation, restoration and enhancement (Cowx, 1994b).

2.1 Conservation

Conservation stocking is undertaken to maintain biodiversity in populations at high risk of decline and/or extinction (Cowx, 1994b). In such situations stocking is carried out with the aim of maintaining a population until pressures adversely affecting conservation status can be addressed or subside. In situations where wild populations are in critical decline, the window of opportunity for conservation of the remaining wild resource may be rapidly closing (O'Reilly and Doyle, 2007) and intervention by stocking may be the best and only option available. In such programmes, the hatchery can be considered to be a living gene bank (Gausen, 1993; O'Reilly and Doyle, 2007). Such conservation stocking is exemplified by application in a number of contexts in several countries. The approach has been adopted to seek preservation of the phenotypically and genetically distinct groups of Atlantic salmon residing in the Inner Bay of Fundy, Canada (Fisheries and Oceans Canada, 2018). It has also been applied in Norway towards conservation of populations threatened by acid precipitation and infection by the parasite *Gyrodactylus salaris* (Gausen, 1993).

Implementation of a living gene bank requires considerable economic cost and robust science-based operating procedures that minimise the negative consequences a hatchery situation can create (O'Reilly and Doyle, 2007), as discussed in due course. Further, as with any supplementation initiative, unless and until the original pressure(s) has been addressed, the chance of success is questionable (ICES, 2017).

2.2 Mitigation

Mitigation stocking is defined as “Stocking conducted as a voluntary action or statutory requirement to mitigate lost production due to an activity that cannot be removed” (NASCO, 2007). This approach aims to offset losses of production in freshwater that are due to anthropogenic impacts and/or recent increases of salmon mortality in the marine environment (Chaput, 2012; Lehnert *et al.*, 2019). A total of twelve anthropogenic stressors acting on salmon populations were identified by ICES (2017): 1) barriers, including but not limited to hydroelectricity production, 2) pollution, 3) water regulation, 4) exploitation, 5) aquaculture, 6) habitat degradation, 7) diseases and parasites, 8) climate change, 9) invasive species, 10) predators, and

11) other uncategorised stressors (e.g. light and noise pollution, shipping) and 12) stocking. Indeed, stocking was listed both as a potential action and a potential stressor, due to the negative impacts such a process may produce. There are a wide range of types of mitigation stocking associated with the diverse set of stressors acting and interacting in different populations. In many cases, due to the inability to remove stressors, such stocking can be significant and long lasting. For example, extensive stocking has been applied to attempt to mitigate for obstruction to free passage of migrating salmon associated with hydro-electricity dams in some cases for many decades (MacCrimmon and Gots, 1979; Parrish *et al.*, 1998; Palmé *et al.*, 2012; Lenders *et al.*, 2016). Indeed, the inputs in some areas are so great that they now represent a larger proportion of the stocks than natural production (e.g. the Baltic Sea where annual releases of ~5 million juveniles represent c. 60% of the total production; ICES, 2018).

2.3 Restoration

The aim of stocking for restoration purposes is to promote the rapid recovery of natural populations that have been reduced in numbers after the cause of the decline has been identified and removed (Aprahamian *et al.*, 2003). In their review of restorative stocking programmes, ICES (2017) found that such programmes can be effective in achieving these aims. Thus, notwithstanding the risks associated with stocking (reviewed below) and if used with due caution, correct planning and evaluation, restorative stocking has been shown to be a useful approach in the managers' toolkit. It should also be noted that, even if such a programme does not reach its ultimate goals, it can still provide a valuable positive impact by reducing short-term pressures while other human-led and/or natural restorative processors are underway, especially in the early stages of recovery (e.g. Milner *et al.*, 2004).

2.4 Enhancement

Enhancement stocking is undertaken to augment the production of wild stocks through the release of hatchery-reared fish (NASCO, 2007), typically to increase recreational and/or commercial fishing opportunities (Utter and Epifanio, 2002). Such stocking is achieved through a number of routes. In some cases, hatchery produced fish are stocked into areas already containing a wild population, with the aim to boost the natural numbers (Bacon *et al.*, 2015). Stocking of fish can also be carried out in areas of a watershed not usually accessible to the wild populations, due to natural barriers and so outside native range (Killinger, 1994), or lack of suitable habitat for certain life-history stages (Armstrong *et al.*, 2003), again with the aim of increasing availability of juvenile habitat and associated carrying capacity of a watershed. Such stocking can also be carried out into rivers in geographic regions where the species is not found at all naturally (MacCrimmon and Marshall, 1968; MacCrimmon and Gots, 1979; Halverson, 2010; Gordeeva and Salmenkova, 2011). Finally, ocean ranching can be carried out using mass releases of juveniles directly into the marine environment, with the aim of completely avoiding the potential bottleneck of juvenile freshwater carrying capacity (Moberg and Salvanes, 2019).

Table 1

Risks mechanisms and impacts associated with hatchery supplementation. A full reference list for each issue can be found in Appendix 1.

Issue	Mechanism/s	Impact
Hatchery		
Broodstock collection	Broodstock mixing, restricted broodstock numbers, disruption of mate choice and reproductive timing, loss of natural production	Loss of genetic diversity, homogenisation of populations, loss of local adaption
Use of non-native stocks	Maladaptation to local environment	Reduced fitness, increased straying, loss of population structure, introgression into wild stocks, decline in numbers following hatchery cessation
Domestication	Adaptation to hatchery, gene expression changes	Loss of fitness in wild, loss of reproductive capabilities, loss of population structure, phenotypic, physiological, behavioural and life history changes
Introduction of escaped farmed fish into broodstock	Collection from wild without screening	Loss of local adaption, reduced fitness
Hatchery adaptation	Epigenetic changes	Altered gene expression, physiological processes, migration, behaviour
Hatchery conditioning	Hatchery rearing causing plastic phenotypic divergence	Changes in growth rate, morphology, behaviour and life history traits
Loss of resilience	Reduced genetic variability	Long-lasting evolutionary impacts and loss of resilience to environmental changes
Environmental		
Competition	Physiological and behavioural interactions	Compromised natural recolonization, reduced

		natural production, ecological disturbance
Displacement	Displacement of wild gene frequencies/stocks	Displacement of wild stocks and replacement with hatchery
Hybridisation (hatchery/wild)	Hatchery fish interbreeding with wild fish	Loss of fitness in wild-born hybrid offspring, loss of population structure, loss of genetically defined traits, changes in catchability
Hybridisation (inter-species)	Increased hybridisation in areas of stocking	Loss of wild reproduction, loss of fitness
Immunocompromisation	Hatchery selection	Reduction in disease resistance in wild population
Enhanced straying	Maladaptation to local environment	Enhanced straying of hatchery inputs
Enhanced predation	Behavioural changes	Attraction of predators to greater resource and/or to less risk adverse hatchery fish which also then impacts wild. Stocked fish may directly predate wild or same or other species.
Introduction of parasites/pathogens	Infections from hatchery transferred to the wild	Mortality / eradication of wild stocks
Anthropogenic		
Overharvest	Fishing mixed hatchery/wild stocks may impact weak/small wild populations	Loss of population structure, decline/loss of wild populations
Sociological impacts	Manipulated natural state	Reduces sense of ‘naturalness’, false sense of security, undermining of incentives and divergence of resources from other management strategies

3. Risks

Whist the aims when stocking fish are to conserve, mitigate or enhance natural populations, there is a large body of research which illustrates the risks associated with such strategies (Table 1, Appendix 1). Such risks fall within three broad categories: those associated with collection of broodstock and production of individuals in the hatchery, environmental impacts when fish are stocked into the wild, and anthropogenic impacts due to changes in behaviour of those who utilise and manage the resource.

3.1 Hatchery issues

Fish produced in hatcheries have been shown to be less fit than wild conspecifics when released into the natural environment (Araki *et al.*, 2008; Christie *et al.*, 2014), even after a single generation in captivity and/or when produced from wild-caught broodstock (Christie *et al.*, 2012a; Milot *et al.*, 2013). Fitness reduction is a result of a number of physiological and genetic processes (Table 1) and introductions of such hatchery fish can result insignificant deleterious impacts on wild genetic integrity (Garcia de Leaniz *et al.*, 2007; Naish *et al.*, 2007; Blanchet *et al.*, 2008; Araki and Schmid, 2010). In turn, and especially over the long term, this impact may result in entire populations of fish that are maladapted to their natural environment (Araki *et al.*, 2007; Henderson and Letcher, 2011) and, as a result could lead to populations that have reduced genetic variability and associated loss of resilience to environmental changes (McGinnity *et al.*, 2009; Sgrò *et al.*, 2011)

Wild salmon are structured into a hierarchy of populations, from the continental to the tributary level (Verspoor *et al.*, 2005; Cauwelier *et al.*, 2018b; Jeffery *et al.*, 2018) and this structure is associated with local adaptive genetic variation (Garcia de Leaniz *et al.*, 2007). Any disruption to local adaptation in the wild stock can lead to an associated loss of fitness and potentially result in an extinction vortex in the wild fish (McGinnity *et al.*, 2003). Mixing of fish from different populations, and the use of non-native fish, both may result in the homogenisation of population structure (Vasemagi *et al.*, 2005; Williamson and May, 2005; Östergren *et al.*, 2021) and associated loss of genetic adaptation (McGinnity *et al.*, 2009). Where broodstock are collected from the wild, numbers used will often be lower than that found naturally. This will result in a loss of genetic diversity, even if all fish are from native populations, which again may negatively impact the diversity and resilience of the recipient populations (Christie *et al.*, 2012b). Mating is also artificially achieved in the hatchery, with disruption of natural mate choice and reproductive timing (Neff *et al.*, 2008; Tillotson *et al.*, 2019) and associated risks to natural genetic variation.

In many instances escapees from aquaculture facilities are found in rivers together with wild fish (Youngson *et al.*, 1997; Green *et al.*, 2012; Wringe *et al.*, 2018; Glover *et al.*, 2019). Aquaculture stocks have been selected over many generations for traits of interest to the farming industry (Gjedrem, 2000; Gjedrem, 2010), have undergone domestication selection to their artificial environment (Vasemagi *et al.*, 2012; López *et al.*, 2018) and may be from areas far distant from the wild populations surrounding them (e.g. Norwegian origin farm stocks outside Norway). As such, aquaculture stocks are genetically and phenotypically very different to wild fish (Teletchea and Fontaine, 2014; Glover *et al.*, 2017) and the fitness of escapees and farm/wild hybrids is much reduced compared to wild stocks (McGinnity *et al.*, 2003; Glover *et* *al.*, 2012; Skaala *et al.*, 2012; Diserud *et al.*, 2017; Glover *et al.*, 2017; Skaala *et al.*, 2019). Inadvertent inclusion of such fish in hatchery production will again result in loss of local adaption and fitness (Glover *et al.*, 2017; Glover *et al.*, 2020).

Fish produced and/or reared in a hatchery will face selection pressures to adapt to their hatchery environment, a process termed domestication, which can occur in as little as a single generation of captivity (Fleming and Einum, 1997; Fraser, 2008; Milot *et al.*, 2013; Christie *et al.*, 2016). In order to flourish in a hatchery environment a wide variety of different processes and behaviours (e.g. aggression, food conversion, predator avoidance, immune response etc) will be under different selection pressures than in the wild. Fish which do well in such conditions will tend to dominate, and selection will tend to drive the stocks away from the wild ideal (Araki *et al.*, 2007; see also Appendix 1). Together with this direct genetic impact of domestication selection on genotype and associated fitness, there is also evidence for epigenetic modifications (changes that affect the genomic structure and regulate gene expression) induced by hatchery rearing, which also provide a potential explanatory mechanism for the reduced fitness of early generation hatchery-reared salmon (Le Luyer *et al.*, 2017; Rodriguez Barreto *et al.*, 2019). Genetic changes associated with domestication have been shown to both reduce the fitness of hatchery fish when stocked into the wild (Fleming and Einum, 1997; McGinnity *et al.*, 2003; Araki *et al.*, 2007; Hutchings and Fraser, 2008; McLean *et al.*, 2008; Araki *et al.*, 2009; Thériault *et al.*, 2010; Thériault *et al.*, 2011), and also reduce the fitness of the recipient wild stock (Araki *et al.*, 2009; McGinnity *et al.*, 2009).

Selection in the hatchery can cause direct genetic responses, however, hatchery conditioning can also cause plastic phenotypic impacts on fish raised in such environments. Processes such as growth rates, morphology, behaviour and life-history traits can all be influenced by such rearing environments (Chittenden *et al.*, 2010). Although not a direct genetic effect, such changes can impact the genetic composition of the wild recipient population in an indirect way through competitive interactions between the hatchery and wild fish. Again then, genetic disruption of the wild population can result with associated fitness implications.

The various genetic impacts of hatchery production will often tend to reduce the genetic variability of a population. While this may have immediate impacts due to loss of fitness of individuals, there is also a longer-term risk associated with a populations and/or group of populations resilience to environmental change. The ability to adapt to such change is reliant on the inherent genetic variation both across (the portfolio effect: Schindler *et al.*, 2015) and within populations (Bernatchez, 2016). Loss of such variation means that a population has no genetic resources upon which to call on in times of environmental change, and as such represents a long-term risk to population viability (McGinnity *et al.*, 2009).

There has been a significant amount of both theoretical and more practical based analysis of techniques to reduce the negative genetic effects associated with hatchery rearing (reviewed in Fisch *et al.*, 2015). Such techniques focus on broodstock selection (e.g. collect from single locally adapted populations; collect enough fish to maximise founder genetic diversity; minimise generations in captivity; minimise domestication selection; screen for escaped farm fish), broodstock spawning (e.g. develop optimal mating scheme such as random, factorial or free mate choice; inbreeding avoidance through various molecular and/or pedigree techniques), and rearing and release (e.g. enriched environments; equalisation of family sizes). Research is still needed however to evaluate the long-term effectiveness of such approaches or to see whether the benefit to the population justifies the cost (Fraser, 2008; Fisch *et al.*, 2015). However, as techniques and technology improve both the theoretical and practical application of such approaches mean some of the negative genetic impacts of hatchery rearing may start to be able to be negated.

3.2 Environmental issues

Stocking of fish into areas of a river where natural production is taking place to try to boost fishery numbers has historically been the most common stocking practice, with the first commercial hatchery being developed on the Rhine in 1852 (Harris, 1978). However, from the early days, doubts about the efficiency of such programmes were expressed (Kennedy, 1988). What little scientific assessment that had been undertaken by the 1970’s suggested that, although 38 organisations were operating hatcheries, their input contributed to less than 2.5% of commercial catches (Harris, 1978). Notwithstanding the significant developments in hatchery practices, scientific knowledge, ecosystem understanding and monitoring programmes in the 50 years since that date, it is interesting to note that in a recent study of enhancement hatchery inputs to the River Spey in Scotland, just 0% – 1.8% of the rod catch was identified as originating from the hatchery between 2018 – 2012 (Coulson *et al.*, 2013). Such findings are perhaps to be expected. In the absence of external stressors, the production of a particular river section is limited by its carrying capacity and availability of broodstock. Fish stocked at or above carrying capacity will lead to increased detrimental competition with wild fish. In addition, when broodstock are taken which would otherwise have gone on to spawn naturally their contribution to natural spawning is removed. As such, it is unsurprising that there should often be little or no increase in fish production (Saltveit, 2006), and that this scenario has been realised across many different attempted enhancement programmes (e.g.

Saltveit, 1993; Fjellheim *et al.*, 1995; Saltveit, 1998; Einum and Fleming, 2001; Fjellheim and Johnsen, 2001 and references therein; Borgstrom *et al.*, 2002; Araki and Schmid, 2010).

It is evident that positive effects of stocking on production can only be realised in a particular location if that location is below carrying capacity and has available spawners to be used as broodstock (Aprahamian *et al.*, 2003). As rivers are highly dynamic systems, this carrying capacity will vary in both time and space (Armstrong *et al.*, 2003) and act with different intensity on different life-history stages in different areas of a system (Malcolm *et al.*, 2019). As such, in many, if not most situations, the limiting factors or bottlenecks for fish production are not well documented (Cowx, 1994b; Saltveit, 2006). In the absence of such knowledge and if accommodation cannot be made for the age-specific capacity of a system, such stocking can result in catastrophic consequences (Saltveit, 2006) for both the hatchery and wild stock, with competitive interactions resulting in reductions in both fitness and juvenile numbers of both types in the system (see examples in Fjellheim and Johnsen, 2001; McGinnity *et al.*, 2009; Araki and Schmid, 2010) and displacement of wild gene frequencies/stocks (Altukhov, 1981; Hindar *et al.*, 1991; Marzano *et al.*, 2003).

A potential stocking enhancement alternative in systems already at or near carrying capacity is to stock fish at life history stages that avoid the age-specific density-dependent bottlenecks that limit production. Such stocking could involve placing ova at uniform densities to reduce local density-dependent mortality; stocking fish into areas that have limited spawning habitat but more extensive juvenile habitat and, what is recently perhaps the most common approach, to capture broodstock and raise offspring to the smolt stage before release.

A significant limitation to the carrying capacity of a system is the availability and distribution of spawning habitat (Taylor *et al.*, 2017; Glover *et al.*, 2018). A combination of factors such as river bed slope, flow, hydraulic and sedimentary variables all interact to define the suitability and, hence, availability this habitat (Moir *et al.*, 1998; Louhi *et al.*, 2008). Thus, in many, if not all, river systems, the distribution of optimal spawning habitat (Louhi *et al.*, 2008) is not uniform (Crisp and Carling, 1989), but is rather a patchy distribution (Moir *et al.*, 1998; Glover *et al.*, 2018). In order to maximise egg to smolt production, hatchery eggs can, in theory, be planted in uniform densities, with the aim of reducing density-dependent mortalities. Quantifying the success of such a process is, however, not straightforward, as outcome is usually measured by smolt and/or adult counts (Glover *et al.*, 2019), which are influenced by numerous factors unrelated to egg distribution. Where it has been possible to study each life history stage in detail, the artificial stocking of ova in a uniform distribution was found to increase juvenile numbers of stocked over wild fish up to the fry stage (Glover *et al.*, 2019). However, strong density-dependent mortalities meant that this population size increase was not transmitted to later parr production (Glover *et al.*, 2019) or smolt output (Bacon *et al.*, 2015). It was concluded that such stocking fails to increase Atlantic salmon production where wild fish populations and suitable habitat remain (Bacon *et al.*, 2015).

An alternative production enhancement strategy is to stock areas of habitat that are below juvenile carrying capacity. Apart from situations where spawning habitat is completely absent and so there is a complete lack of juvenile fish (see below), it is difficult to disentangle the various factors that may result in juvenile habitats being below carrying capacity. The intense density-dependent mortality seen in juvenile salmon (Vincenzi *et al.*, 2012; Walters *et al.*, 2013), especially at the earliest life history stages (Einum *et al.*, 2006), means that sub-optimal juvenile numbers may be not be the result of a lack of spawning opportunities but rather from some other extrinsic stressor. If so, stocking may achieve little benefit (ICES, 2017). The added difficulty of accurately quantifying the juvenile carrying capacity of a system (Uusitalo *et al.*, 2005) also raises the danger of overstocking, increased competition and associated negative consequences to both stocked and wild fish (Cowx, 1994b).

In order to bypass restrictions that a river imposes on production, either from natural (such as intrinsic carrying capacity) or anthropogenic (through a variety of stressors) sources, fish can be reared and released into the environment as smolts (Isaksson *et al.*, 1997; Moberg and Salvanes, 2019). The goals of such programmes are to avoid early age class competitive interactions and increase captures in commercial and/or recreational fisheries by boosting production above that which could occur naturally (Isaksson, 1988; Mustafa *et al.*, 2003). Such ranching programmes have been utilised extensively in an effort to boost fisheries of several salmonid species, including various Pacific salmon species in North America and Japan (Mustafa *et al.*, 2003; Moberg and Salvanes, 2019). It is estimated that around 40% of the salmon in the Pacific Ocean are of hatchery origin (Ruggerone and Irvine, 2018). As with many hatchery programmes, however, and despite the long history and large scale of such hatchery production in the Pacific, their efficiency as a tool for increasing production has rarely been rigorously demonstrated (Naish *et al.*, 2007; Amoroso *et al.*, 2017). Whilst salmon numbers in the Pacific have increased significantly over the period that hatchery inputs have been operating; there has, at the same time, been a major change in productivity in the North Pacific boosting natural production (Amoroso *et al.*, 2017). Disentangling the influence of hatcheries from that of natural variation is crucial to understanding the outcome of hatchery intervention. Where this has been attempted, the findings suggest that positive enhancement effects of the ranching are relatively minor (Morita *et al.*, 2006; Scheuerell *et al.*, 2015; Amoroso *et al.*,

2017) and context-dependent (Kaev, 2012). Further, even if there may be some small enhancement benefit to the fishery, ranching programmes have the potential to negatively impact the wild stocks that they interact with and actually reduce productivity in the wild stocks (Hilborn and Eggers, 2000; Amoroso *et al.*, 2017) through mechanisms, such as replacement (Hilborn and Eggers, 2000), together with enhanced straying rates (Brenner *et al.*, 2012) and associated negative ecological and genetic interactions (Jasper *et al.*, 2013).

In the North Atlantic, apart from some limited and often experimental programmes, Iceland has seen the most significant salmon ranching programme (Isaksson *et al.*, 1997; ICES, 2019). Ranching for recapture at the river of release was initiated by the Icelandic government in 1961 (Arnason, 2001), with a number of large-scale facilities operating in the 1980's and 90's (Isaksson *et al.*, 1997). However, due to issues surrounding significant straying, illegal fishing, and especially poor economic results (Arnason, 2001), the activity has now virtually ceased, is restricted to two rivers and productivity has decreased from a high of 499 tonnes in 1993 to just 28 tonnes in 2017 (ICES, 2019).

A final mechanism of commercial stock enhancement which avoids completely juvenile competitive interactions is to stock fish outside their natural ranges. Such an approach covers stocking both within river systems and in regions/oceans outside the species' native range. Some rivers already harbour wild populations of salmon, but include natural barriers, such as waterfalls, which mean that parts of the system have always been inaccessible to wild fish. Fish can be stocked in these inaccessible areas in order to maximise production for the river system as a whole beyond that which could occur naturally. Assuming the suitability of habitat and the ability for downstream passage of the barrier; such a strategy would undoubtedly increase the numbers of migrating smolts, due to the increased amount of productive habitat available. However, such a programme will also have introduced changes to the natural ecosystems in stocked areas, especially through competitive interactions with other fish species (Kennedy, 1982; Hearn, 1987; Berg *et al.*, 2014). Such interactions have been shown to have the potential to change the distribution and depress the natural production of the native species following stocking with salmon (Kennedy and Strange, 1980; Kennedy and Strange, 1986) . Such stocking practices may also result in negative impacts on wild fish populations naturally spawning in areas below the barrier, as any returning spawners will be unable to migrate past the barrier and if all are not collected may stray into neighbouring populations and introduce restricted/novel genotypes into these populations (e.g. Östergren *et al.*, 2021).

An extreme example of stocking fish outside their natural range is the trans-oceanic stocking of Pacific pink salmon (*Oncorhynchus gorbuscha*) leading to the establishment of self-sustaining populations in the Atlantic White and Barents Sea areas (Gordeeva and Salmenkova, 2011), resulting in a significant commercial fishery (reviewed in Niemelä *et al.*, 2016). Hand-in-hand with this commercial 'success' came the potential and realised negative impacts on native salmonid stocks of other species, especially Atlantic salmon. Significant straying of pink salmon has been observed, especially into areas immediately surrounding the stocked region (e.g. Norway: Mo *et al.*, 2018) but also throughout the whole North Atlantic (e.g. England, Scotland, Ireland, Iceland: Bartlett, 2017; Armstrong *et al.*, 2018; Millane *et al.*, 2019; Sandlund *et al.*, 2019). Associated and ongoing risks of competitive interactions, pathogen and parasite transfer, unbalanced nutrient inputs and economic impacts on recreational fisheries (Mo *et al.*, 2018) across the North Atlantic means such stocking practices have resulted in one of the most significant risks yet seen with any such enhancement programme.

Hybridisation of hatchery fish with wild conspecifics is a further potential risk associated with stocking programmes. If stocked fish breed at either the parr stage or as returning adult spawners again this can negatively impact the fitness of the wild stocks. Such outcomes are again the result of the disruption of natural genetic population structure (Östergren *et al.*, 2021) and loss of genetic diversity (Marzano *et al.*, 2003) associated with the hatchery inputs. Impacts can be severe, and cumulative, and the depressed recruitment and disruption in the capacity of natural populations to adapt to environmental change raises risks to the long term viability of such populations (McGinnity *et al.*, 2009). Together with the problem of inter-specific hatchery/wild hybridisation also comes the risk of intra-species hybridisation. In areas which have seen hatchery stocking, especially where native wild populations are depressed (Garcia de Leaniz and Verspoor, 1989), or stocking takes part outside the native range (Verspoor, 1988), enhanced rates of intra-specific hybridisation may occur with associated potential future depression of recruitment.

Introduction of fish conditioned or selected in the hatchery can cause changes in their behaviours in the wild on top of the direct competitive interactions. Hatchery reared individuals are more aggressive and less risk adverse than wild counterparts (Johnsson *et al.*, 1996). Such behaviours, taken together with an increased resource due to stocking, has been shown to risk the attraction of predators (Collis *et al.*, 1995). In turn, this may lead to enhanced predation not only on the stocked fish but also on the wild with associated negative impacts on survival (Kennedy and Greek, 1988; Shively *et al.*, 1996; Walter *et al.*, 2005).

There is always a natural level of straying of a proportion of wild fish away from their natal spawning grounds (Keefer and Caudill, 2014). Such straying may be enhanced in hatchery fish (Jonsson *et al.*, 1991a), and/or stocked fish displaced from their rearing site for release (Quinn, 1993). If fish are stocked as mitigation for a barrier in the river, there is also the risk that such fish will stray into populations below the barrier on return and again disrupt local genetic structure. Stocking thus carries risks not only to the enhanced population, but also those in surrounding areas.

A final environmental risk associated with stocking is the inadvertent transfer of parasites and/or disease from the hatchery to the wild. Diseases which become problematic in the hatchery may then be enhanced in the wild as has been seen with Bacterial Kidney Disease (BKD) caused by *Renibacterium Salmoninarum* in hatcheries stocking chinook salmon and steelhead in the Columbia river system (Elliott *et al.*, 1997). By far the biggest such impact has been the introduction and spread of the ectoparasite *Gyrodactylus salaris* through the stocking of infected hatchery fish in Norwegian salmon populations, and which have devastated a number of rivers (Johnsen and Jensen, 1986). Extreme care careful monitoring, and a disease-free certification process should thus be carried out in any hatchery planning to introduce fish into the wild.

3.3 Anthropogenic impacts

The hatchery environment can not only change the behaviour of the stocked fish, but it can also change the behaviour of those exploiting the resource. Increasing a stock of fish such that it may be target for fishery and/or angling exploitation risks impacts not only on the wild remnants of the stocked population, especially if they are not easily distinguished through some sort of tagging, but also on neighbouring populations. In both the marine and freshwater environments fish exists in mixed river and/or population stocks. Exploitation of one stock can thus risk many stocks through by-catch as exploitation is increased targeted at stocked individuals (Hilborn, 1985; Beamish *et al.*, 1997; Unwin and Glova, 1997). Such exploitation may be offset to a degree through marking of hatchery fish using mechanisms such as adipose clipping allowing hatchery fish to be identified and wild avoided (Saltveit, 2006; Bronte *et al.*, 2012; ICES, 2018; WDFW, 2019).

Changes in behaviour can also be associated with changes in perception of both the resource and the environment in which it exists. Many people view wilderness as “the one place in our increasingly human-dominated world that is specifically designated to be left alone and not manipulated for human desires“ (Landres *et al.*, 2001). Any act which compromises this status can negatively influence perception of the wildness of both the environment and the fish resource. Catching a large stocked fish is, in many people's opinion, not the same as catching a truly wild individual. This may lead to lower catches if stocking for enhancement is not undertaken, and while this may suit those who view wilderness in this way, it may be sub-optimal to those who simply want to enjoy the environment while catching fish of any source.

There is a further risk that the operation of a hatchery becomes an end in itself due to the perception, often with no evidence, that stocking is bringing benefits to a system through the addition of fish. In the absence of such evidence, the rationale behind the programme rests on perception of success, tradition and the need to preserve employment opportunities. In reality stocking carries risks, as have been outlined, and may in fact be negatively impacting recipient populations. Even if such risks are not realised, in the absence of any proved benefits resources (and indeed employment) may be diverted from ecosystem management strategies which may result in better outcomes (Burton and Tegner, 2000; Carr *et al.*, 2015).

4. The development of a stocking programme

Careful specification and application of a stocking programme is required to prevent doing more harm than good (Cowx, 1994b; Aprahamian *et al.*, 2003; Naish *et al.*, 2007; NASCO, 2007; Araki and Schmid, 2010; Young, 2013). The successful implementation of such a programme requires the development of a strategic approach that identifies the problem, defines the objectives, orientates the implementation to meet the goals, and effectively monitors the outcomes. The various steps for consideration in setting up such a programme are set out below and outlined in Fig. 2 (Cowx, 1994b; Cowx *et al.*, 2012).

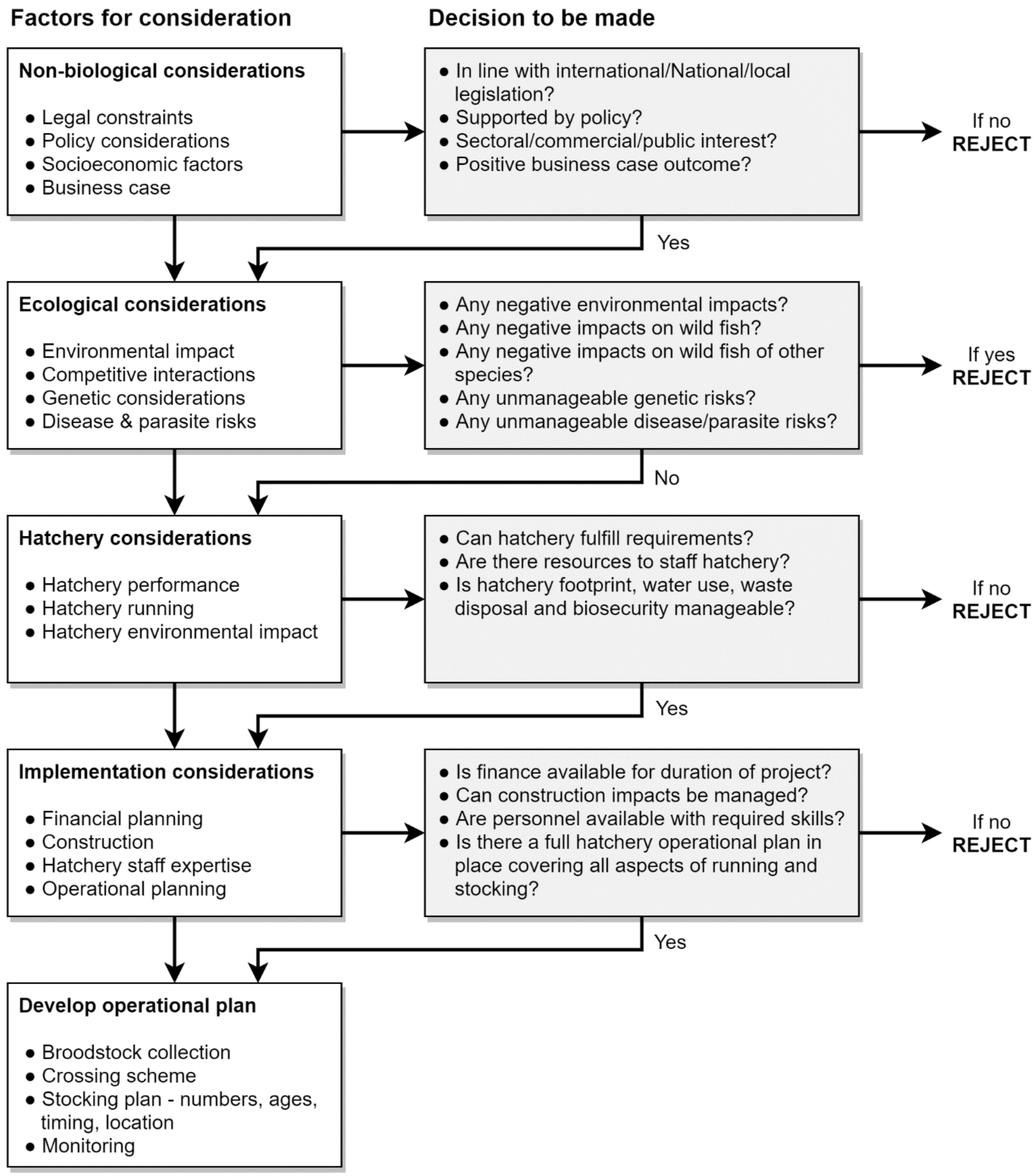

Figure 2 Factors for consideration when setting up a stocking programme (modified after Cowx *et al.*, 2012; Anon, 2013).

4.1 Non-biological considerations

A stocking programme, as with any management intervention, must be performed legally. Planned activities must thus be compliant with any relevant legislation at the international, national and local levels. Such legislation may cover all stocking of fish in a country (e.g. the complete prohibition on stocking in Wales: Natural Resources Wales, 2014) or specific activities at specific times in specific places. It may not even be directly based on stocking of salmon, but rather on the impact of such activities on other protected species and/or habitats. It is vital, therefore, that a thorough evaluation be made of the relevant legislation.

Similarly, although not defined in primary legislation, there may be policies applied by regulatory bodies and/or management organisations which are relevant to a planned stocking programme. Again, these may cover specific activities/times/places but also the aims of any proposed programme. For example, there may be a ban on stocking for certain purposes (e.g. enhancement) while other types may be allowable or even encouraged (e.g. conservation). Such policies and associated guidance must again be carefully considered before any programme is implemented.

In many historic situations, socioeconomic drivers have been of particular importance when setting up a stocking programme. Societal value and economic income from salmon fishing in many areas has been high and, with recent declines in the available resource, the drivers for management intervention are also high. Such pressure must, however, be balanced by the best scientific advice available to try to achieve agreement between the drivers and the science, as well as consensus between those on differing sides of the debate. Achieving such a consensus is not, however, straightforward as was well illustrated by the discussions surrounding the recent stocking policy development in Wales which resulted in entrenched and antagonistic positions being developed by different groups of stakeholders (outlined in Harrison *et al.*, 2019b).

Finally, a stocking programme must have a comprehensive business case. The funding, planning, aims, operation and monitoring must be well defined at the outset. Such a business case does not have to be financially viable in the same way as a traditional one and, indeed, a stocking programme may be a financial loss-making enterprise even if the full economic benefits are calculated, yet still be a conservation success. It does, however, have to be based on a sound financial plan for operation throughout the lifetime of the planned intervention, whether this is through regulatory body funding, direct cash injection by interested parties, fundraising, and/or other avenues. Full costs should thus be defined at the outset and yearly breakdown of operational costs and available funds outlined at the planning stage.

4.2 Ecological considerations

As with any anthropogenic environmental intervention, careful consideration must be made as to the ecological risks of such actions over and above that of the focus stocks (Holmlund and Hammer, 2004). In order to assess likely impacts and as part of the plan development for the stocking project, initial ecosystem-wide analysis of the site of stocking would be required to examine the potential effects of the action on both wild conspecifics and other species taking account of competition and predator/prey interactions. Through the evaluation of this analysis, site-specific issues could be addressed and mitigation solutions, as well as, monitoring strategies brought into the plan.

4.3 Hatchery considerations

Establishment of a stocking programme necessitates the development of a hatchery operation. Examination of the full implementation and running of such an establishment is beyond the scope of this review. However, it is imperative during such development that proper consideration is given to the aims of the programme and the ability of the hatchery to meet these aims. There is little point in developing a hatchery before a thorough stocking plan has been developed, which will include a definition of the required numbers of fish, the capacity to keep separated different genetic groups of fish, and the ability of the hatchery to meet these requirements. It is also imperative that the staffing and other resource implications are defined and the environmental impact of running the hatchery is carefully considered. This will include disruption during building and maintenance of the physical structure, and also, importantly, impacts from the discharge of the facility (Michael, 2003; Tello *et al.*, 2010). Fish and food waste will require monitoring and biosecurity of both fish and potential diseases and parasites established (Lillehaug *et al.*, 2015).

4.4 Implementation considerations

It is perhaps obvious that a hatchery development, as with any other business, requires a detailed financial plan (Cowx *et al.*, 2012). Such a plan should cover both the construction and running of the facility, with full costings of infrastructure and staffing for the duration of the project. A hatchery represents a significant investment and may mean substantial capital input and ongoing running costs. It is thus vital that a realistic commercial plan is put in place to cover the financial aspects of the operation. The running of such a facility requires particular expertise and, again, there should be a plan in place to either obtain or develop the required skills.

4.4.1 Operational plan

The running of a hatchery supplementation programme requires a detailed operational plan covering all aspects of the intervention. The plan should cover the various practical aspects of the operation (outlined in Fig. 3) and be reviewed regularly to ensure the operation is following the planned trajectory and/or if the plan requires alteration in the light of new information. In order to ensure best practice, it would perhaps be helpful, at both the planning and review stages, to take independent advice and oversight from outside experts.

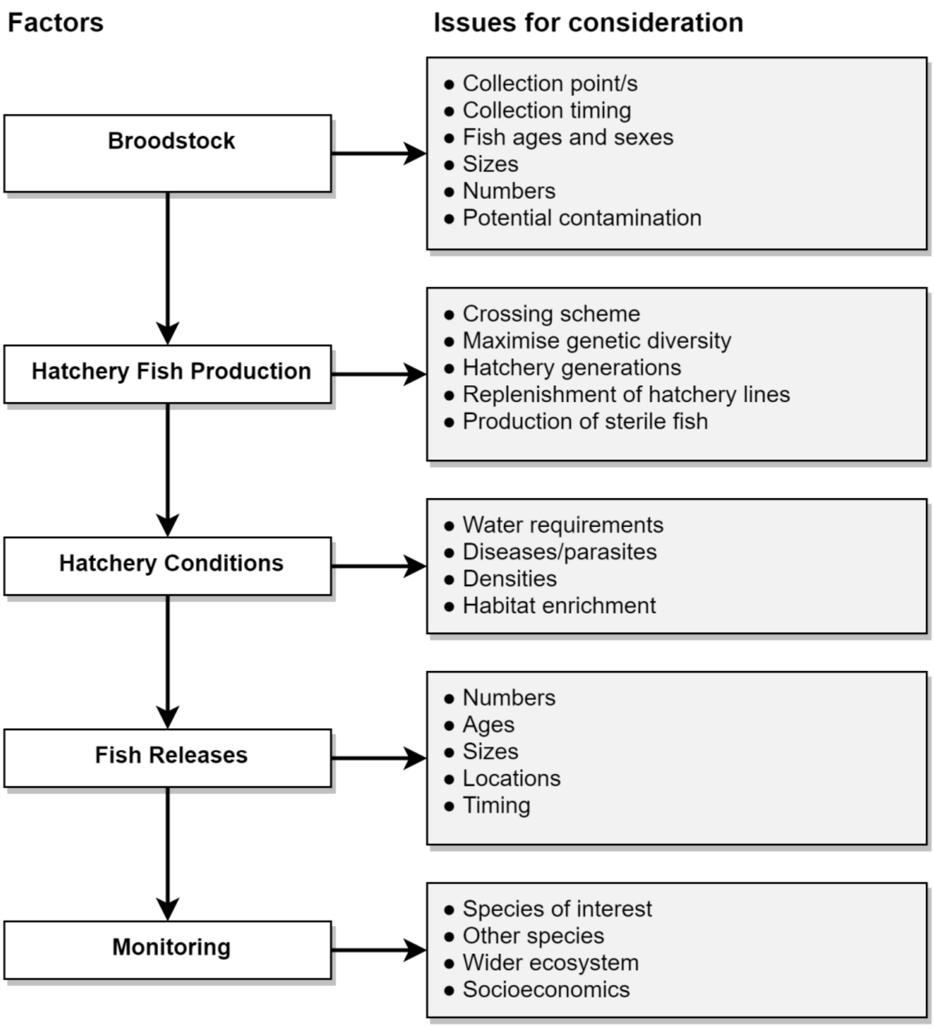

Figure 3 Factors for consideration when planning a hatchery operation.

4.4.2 Broodstock

The hatchery will be utilising wild-caught broodstock and careful consideration is thus required to determine the impact of removal of these fish from the wild population. It is often the case that supplementation programmes are undertaken when wild stocks are low or falling. In such cases, care must be taken to avoid significant additional negative impacts on the stocks remaining (McElhany *et al.*, 2000). In the absence of an identified stressor but with the wide body of evidence showing the reduced fitness of hatchery-produced fish compared to wild (Jonsson *et al.*, 2019), natural spawning should be prioritized where possible. While, in some cases where specific stressors have been identified (e.g. wild habitat loss, ecological pollution, parasite impacts in the wild) (Gausen, 1993; Hesthagen and Larsen, 2003;

O'Reilly and Doyle, 2007; ICES, 2018; Soininen *et al.*, 2019), the most favourable option may be to remove broodstock fish to the hatchery, in many other situations (e.g. where conditions in the wild are still favourable for freshwater production and the system is not at carrying capacity), it will be best to maximise wild production by allowing natural spawning.

A further factor of importance when evaluating the impact of broodstock removal from wild stocks is the structural relationships between populations and sub-populations which can change over time as stressors such as marine survival vary both within and between years (ICES, 2019). This may influence how broodstock selection can be organised. i.e. in poor periods of survival sub-population diversity is likely to fall as the smaller sub-populations are impacted by increased influences of straying from larger adjacent populations (Consuegra *et al.*, 2005). Such impacts may result in a loss of significant population differentiation and a homogenisation of sub-populations. In turn this may mean that is becomes possible to increase the extent of areas available for collection of broodfish without deleterious effect to the existing new population structure. However, below a certain critical threshold, populations are very sensitive to any changes. Removal of members of a small sub-population may take them over the brink making it unviable and leading to possible extinction of that sub population. Care must thus be taken before such an approach is attempted and carful analysis of the sub-population structure undertaken.

Following consideration of the ability of the wild stock to tolerate removal of broodstock fish for the hatchery, the next step is to ensure that collection is carried out in such a way as to maximise the fitness of the offspring produced. Determining where to collect the adult fish is sometimes simple; for example, if a system has a dam preventing upstream movement then stocks can only be taken as close as possible below the dam. This does not mean however, that the fish will actually represent fish from the population/s of focus, due to a degree of straying that occurs during adult return spawning migrations (Malcolm *et al.*, 2010; Keefer and Caudill, 2014). If the barrier is towards the head of the river and/or on the main stem, fish from many tributaries and/or rivers may be captured, with subsequent hatchery production resulting in homogenisation of regionally differentiated, locally adapted populations (Williamson and May, 2005; Östergren *et al.*, 2021). Interbreeding between fish from different locally adapted populations can lead to negative effects on survival and fitness of the offspring, a process defined as outbreeding depression (Fraser *et al.*, 2010; Houde *et al.*, 2011).

In cases where there is no single barrier to migration, the decision as to where to collect fish is not a simple one, due to the many locally adapted populations that may be present in a system (Taylor, 1991; Garcia de Leaniz *et al.*, 2007) members of which may be migrating through different points in the system at different times (Stewart *et al.*, 2006). Fish taken from the mainstem of a river may capture much of the genetic variation in a system. However, the production of crosses with such fish will result in mixing of stocks with, again, the associated risk of loss of local adaptation through outbreeding depression (Manhard *et al.*, 2018). At the other extreme, fish taken from a single/small tributary may miss much of the available wild genetic variation, and subsequent crossing may result in loss of fitness through inbreeding depression (Frankham, 2005). The degree to which either inbreeding and/or outbreeding impacts fitness may be highly unpredictable, even at small genetic distances. As such, there is a need to evaluate the relative risks of inbreeding and outbreeding on a case-by-case basis (Houde *et al.*, 2011).

A second factor to take into consideration is when to take broodstock from a system. Fish return to their natal spawning grounds throughout the year and these adaptive genetic differences associated with run timing are population-specific (Vähä *et al.*, 2011; Cauwelier *et al.*, 2018a). Therefore, unless collection is on the actual spawning grounds during spawning season, there is a danger of missing stock components if all fish are taken at a single time point. In order to capture the full component of the stock, it might be the case that multiple collections take place throughout the year. This does, however, raise the potential problem of shortage of the required number of fish, if numbers are still required late in the season but no fish happen to appear at this time. As such, a careful analysis of the migratory timing of the population of interest should be undertaken and a plan developed to attempt to maximise variation in time of return in order to prevent unintentional selection away from natural patterns (Ford *et al.*, 2006).

A further complexity to the collection of broodstock is that populations are comprised of fish of different ages and sexes (Palstra *et al.*, 2009). In order to maximise genetic diversity, consideration should be made as to the representation of these different groups in the broodstock. The age a fish returns to breed has a significant genetic component (Ayllon *et al.*, 2015; Barson *et al.*, 2015; Aykanat *et al.*, 2019). Fish of different sea ages should thus be collected in proportions similar to the wild stocks and sex ratios matched to known spawning activities (e.g. Taggart *et al.*, 2001; Jones and Hutchings, 2002). Further, as precocious male parr are known to fertilise a significant proportion of eggs (Saura *et al.*, 2008), they should also be collected and used as broodstock. This will maximise the number of breeders to produce the next generation and result in a large effective population size (Garcia-Vazquez *et al.*, 2001).

Knowledge of the local biology of the wild fish when collecting broodstock is vital for capturing and maximising natural variation, thereby ensuring that the stocked offspring represent the wild population as much as possible. However, anglers like to catch big fish and so it is tempting to select the largest fish when choosing broodstock. However, this act alone will produce an unnatural directional selective pressure on the stocks, as it is well known that size is important in mate choice in salmonids (Fleming, 1996; Auld *et al.*, 2019) and has evolved to an optimum in a particular population (Jonsson *et al.*, 1991b; Roni and Quinn, 1995). Thus, again, in order to maintain genetic diversity, a representative selection of fish size at age should be used.

Following determination of where, when and what to collect as broodstock, sufficient numbers should be collected to match the aims of the programme with regards to production but also to minimise the reduction in genetic variation that results when a small subset of a larger population is used as broodstock (founder effects) (Frankham, 2010; Witzenberger and Hochkirch, 2011). This may seem an obvious step, but to avoid situations where either not enough fish are available to meet conservation goals or excess fish are removed from the wild, planning is required to match requirements to objectives. Careful consideration should be given to the range of fish to be collected and the numbers of eggs likely to be produced from fish of a given size using length/fecundity relationships derived from the stocks of interest. Only then can evidence-based broodstock numbers be scientifically justified.

In many areas, a particularly important consideration for hatchery managers when utilising wild-caught broodstock is the risk of contamination of hatchery lines through the use of broodstock that have either themselves escaped from aquaculture facilities or are hybrid offspring of wild fish and farm escapees. It is imperative that broodstock are screened to ensure the fish are not contaminated by aquaculture stocks in areas where there may be impacts from escaped farm fish. There are genetic tools available that can distinguish between farm, wild and hybrid fish (Karlsson *et al.*, 2014; Gilbey *et al.*, 2018; Wringe *et al.*, 2018). Such techniques can be performed relatively rapidly and, so, could be employed wherever broodstock are retained, even if only for short periods. In other cases, where fish are captured and immediately stripped, post-crossing evaluation could be performed and groups of eggs produced from contaminated parents destroyed.

4.4.3 Hatchery fish production

Approaches to achieve the goal of preserving genetic diversity in the hatchery depend on the goal of the supplementation programme. There are two components to preserving genetic diversity: (1) maximising effective population size, and (2) using non-random mating to increase the diversity of genotypes above that expected from random mating (Fisch *et al.*, 2015). The crossing scheme employed in any particular situation should thus be carefully considered. Significant research has been undertaken on this subject (reviewed in Fisch *et al.*, 2015) and considerations include whether to use random or non-random mating, whether to mate single pairs only or use a factorial design, whether to monitor relatedness to avoid sibling-crosses and/or minimise inbreeding, whether to allow free mate choice, and whether to equalise family sizes. The final crossing design decided on will thus have to match available broodstock numbers with conservation requirements and resources available for pedigree monitoring and/or fish rearing. As with the other aspects of setting up a supplementation programme, a detailed crossing scheme plan should be produced before operations commence, following careful review of the available scientific guidance.

Consideration should also be made with regards to the duration that broodstock will be kept in captivity, as well as whether a number of offspring from subsequent generations will be used as broodstock. This is important, as it is well known that, when a stock is retained in a hatchery situation, it is subjected to domestication selection and associated loss of fitness in the wild (Fleming and Einum, 1997; Lynch and O'Hely, 2001; Frankham, 2008; Fraser, 2008) and that, though such fitness reductions can occur within a single generation (Christie *et al.*, 2012a; Milot *et al.*, 2013; Christie *et al.*, 2016), the more generations a stock has been under this selection, the lower the fitness in the wild becomes (Berejikian and Ford, 2004; Araki *et al.*, 2008; Christie *et al.*, 2014; Minegishi *et al.*, 2019). Taking such observations into consideration, it is clear that, if possible, stocking should take place using F1 offspring of wild-caught broodstock. This will reduce any negative fitness impacts of captive rearing. However, in some cases, for example if there is limited wild broodstock, using subsequent hatchery generations may be justified. Again, plans should be developed on a case-by-case basis, depending on the available resources and best scientific advice for the specific situation and supplementation aims.

In certain stocking situations, where, for example, the aims are to enhance stocks for recreational and/or commercial exploitation, consideration should also be made to the possibility of producing and stocking with sterile fish. Sterile (triploid) fish can be produced by heat shocking (Crozier and Moffett, 1989) or pressure treating (Kozfkay *et al.*, 2005) eggs and is now used widely for stocking various species of trout (e.g. Scheerer *et al.*, 1987; Chatterji *et al.*, 2007; Scott *et al.*, 2014). New gene-editing techniques are also becoming available to produce sterile fish (e.g. Dankel, 2018) that may also become of use in the future (especially in hatcheries producing fish for aquaculture purposes). The stocking of such fish will remove the potential direct genetic impact of hatchery fish breeding with wild stock and associated significant negative impacts. However, indirect genetic effects, through mechanisms, such as competitive interactions (Santostefano *et al.*, 2017), mean careful consideration is still required.

4.4.4 Hatchery conditions

Running a hatchery brings the usual practical considerations around water use, waste management, disease and parasite control and biosecurity of fish. The aims of the hatchery are to produce fish that have maximum fitness when released into the wild. As such, consideration should be made into the conditions under which the fish will be raised and whether measures can be undertaken to maximise such fitness. There is much evidence that raising fish in an ‘enriched’ environment leads to enhanced fitness when released into the wild (Flagg and Nash, 1999; Hyvärinen and Rodewald, 2013), as an enriched environment leads to impacts on numerous physiological processes (Crank *et al.*, 2019 and references therein). Enrichment possibilities include but are not restricted to: 1) enhancing habitat complexity by providing matrix substrates and darkened environments; 2) promoting development of body camouflage coloration by creating more natural environments, such as overhead cover and in-stream structures and substrates; 3) conditioning fish to bottom orientation by positioning food delivery low in tanks; 4) altering water flow velocities to exercise fish and so enhance predator avoidance; 5) improving foraging by supplementing diets with natural live foods; and 6) adjusting rearing densities to more natural spatial distributions (Flagg and Nash, 1999 and references therein).

4.4.5 Fish releases

Important considerations for any stocking programme are when, where, how many and at what age to release hatchery stocks. Again, such decisions will be based on an interaction of conservation aims, river system characteristics and practicalities. An important decision for successful stocking is determining age-specific carrying capacity, natural production and setting a corresponding stocking rate (Solomon, 1985). Matching numbers of stocked fish with available resource is critical in order to both promote maximum production from the system and fitness of fish but also to prevent negative effects on wild stocks through impacts on resource availability (Aprahamian *et al.*, 2003 and references therein). Age-specific juvenile carrying capacity can be estimated (e.g. Malcolm *et al.*, 2019) and location specific stocking densities matched to this after taking into account natural production.

The age at which fish should be stocked is, again, another balance between survival and resources. It is obviously much cheaper to stock fish at an early stage, perhaps even as ova, rather than to go through the expense of rearing them to juvenile or smolt stages. The younger the fish are at stocking, the better their adaptation to the wild is likely to be (less domestication selection) and so the smaller the difference in individual expected post-smolt survival compared to wild fish will be (Salminen *et al.*, 2007). However, this intrinsic benefit is offset by the fact that rearing fish in a hatchery to later ages avoids the extremely high natural mortality that occurs during early life stages in the wild (Ware, 1975; Gee *et al.*, 1978; Good *et al.*, 2001). Survival of stocked fish of different ages and life history stages varies greatly (see Table 9 in Aprahamian *et al.*, 2003) and so, again, analysis should be performed and related to the specific goals and resources available to the supplementation exercise.

Although the size of stocked fish will be associated with age, it is also important that fish are stocked at appropriate age-specific sizes. Wild juvenile salmon size-at-age has evolved to maximise fitness in local conditions (Swansburg *et al.*, 2002) and size is important in defining many developmental life history traits, such as precocious maturation (Baglinière and Maisse, 1985; Thomaz *et al.*, 1997) and smolt age (Metcalfe *et al.*, 1989; Heggenes and Metcalfe, 1991; Pearlstein *et al.*, 2007). Stocking of often well-fed large size-at-age fish thus has the potential to disrupt natural competitive interactions in the wild. However, there may also be logical reasons to stock with fish at larger size-at-age than wild fish, depending, again, on the aims of the supplementation programme. If, for example, stocking is with sterile fish in a put-and-take fishery such as with trout, then anglers may want to catch larger individuals. Also, as early salmon post-smolt mortality is high (Thorstad *et al.*, 2012; Chaput *et al.*, 2018) and strongly influenced by size (Salminen *et al.*, 1994; Saloniemi *et al.*, 2004; Jokikokko *et al.*, 2006; Gregory *et al.*, 2019), it may be possible to boost hatchery fish survival by the release of larger better conditioned smolts (Saloniemi *et al.*, 2004).

A further consideration for any supplementation programme is where to stock the fish. In some cases, this may be determined by particular constraints (e.g. dams or other barriers), whereas, in others, careful planning should be undertaken so as not to negatively impact wild recipient populations. It is vital that the carrying capacity of the system is taken into consideration when planning where to stock (Kelly-Quinn and Bracken, 1989). Small numbers of fish stocked uniformly across systems or in areas of known low local densities will thus enhance the likelihood of positive outcomes. However, even if such careful considerations are taken, the strong natural juvenile density-dependent mortality may mean positive impacts may not be realised (e.g. Glover *et al.*, 2018).

The timing of releases is also of importance in ensuring maximum production from the programme. Stocking in the spring has been found to be 4-12 times more efficient than in the winter (Cresswell, 1981; Aass, 1993). Ideally, fish should be released when temperatures and flow are relatively low and productivity is high, but not during spawning period (Cowx *et al.*, 2012). Stocking in spring and/or early summer is thus preferable to allow fish to acclimatise before overwintering. Together with considerations as to whether to stock at a single point (spot planting) or distributed more widely (scatter planting), enhanced success may be obtained if fish are introduced using 'trickle planting' (i.e. releasing batches of fish over an extended time period) (Cowx, 1994a). Trickle planting can reduce competitive interactions by reducing over-dispersion of released fish and, as such, scatter and trickle planting should be preferred over spot planting (Berg and Jorgensen, 1991; Fjellheim *et al.*, 1993; Cowx *et al.*, 2012). As with other aspect of a stocking programme, however, the resources to enable stocking over extended periods must be balanced by the likely enhancements in success rates through such actions.

4.4.6 Monitoring

Once a stocking proposal has been accepted and, as part of the project plan development, all projects should have the methodology in place to enable adequate monitoring of progress and, ultimately, success or failure of the intervention (Cowx *et al.*, 2012). While the objectives of a stocking programme should be clear and set out in the project plan, it is often the case that the lack of suitable monitoring programmes means the efficacy of the programme and the ability to detect impacts or attribute improvements directly to the stocking is lacking (Cowx, 1994b; Waples *et al.*, 2007; Bacon *et al.*, 2015; Glover *et al.*, 2018). Monitoring is important, not only to inform managers of the efficiency of the programme underway but also to inform the development of future programmes of a similar nature.

In order to effectively monitor a stocking programme a baseline is required to which any changes may be compared. Ideally this should cover a number of years and so be able to capture the variations in the various metrics under investigation. That said , certain circumstances, such as imminent extinction, may require a more pragmatic approach to collect the best data achievable in the time available. Cowx *et al.* (2012) outlined a series of factors to be included in a stocking monitoring programme, which should run over an appropriate time-scale and include technical, ecological, genetic and social considerations. They suggested these should cover:

- changes in production trends of stocked/resident fish species
- changes in the genetic integrity of stocked/resident fish species
- changes in growth performance of stocked/resident fish species
- changes in species and catch composition
- impacts of latent disease and parasites

- impacts on the habitats (e.g. loss of aquatic vegetation, changes in the composition of aquatic vegetation, increases in dissolved solids and turbidity) of recipient ecosystems
- impacts on the trophic dynamics of recipient ecosystems (e.g. changes in the quality and quantity of plankton communities, increases in single age groups of particular fish species, changes in the quality and quantity of benthic organisms)
- changes in the socioeconomic conditions of people related to the fisheries

Monitoring programmes should thus seek to determine not only how well ongoing supplementation meets the original aims of the project with regards to the species of interest but also look into the impacts on both the wider ecosystem and the socioeconomics of the people and communities involved. Such a monitoring programme will enable decisions to be made at strategic points in the programme as to whether to continue as planned, revise plans and/or stop the inputs altogether, if either negative impacts are detected or realised outcomes are not meeting projections. As with all aspects of the programme, a science-based monitoring programme should be included as part of the project proposal.

5. Cost / Benefit analysis

To estimate the cost and benefit of a supplementation programme is a task that, although it should be attempted, may, in practice, be difficult to perform. The capital costs of running the programme can relatively easily be defined, however, the various other associated costs and especially benefits, may be both difficult to accurately measure and be, to a degree, subjective (Table 2).

Table 2

Factors to be included for consideration when performing a cost/benefit analysis.

Costs	Positive	Negative
Capital	Injection of money into local economy	May be significant with no guarantee of success
Operational	Injection of money into local economy, jobs	Ongoing uncertainties about long term funds
Broodstock	Increase survival of offspring	Loss of wild spawning
Ecological	Restore natural fish numbers	Competition, pathogens, resources
Genetic	Conservation of genotypes	Inbreeding, outbreeding, loss of population size
Fitness	Conservation of phenotypes	Loss of fitness of hatchery and wild fish
Conservation	Production, conservation, restoration	Displacement of effort
Economic	Fishery, ancillary industries	Displacement of effort
Sociological	Appearance, community, history	Expectations

It should also be noted that, even if all stakeholders have the same conservation, restoration and/or enhancement aims (which may not always be the case), different conclusions may still be drawn from the same available cost/benefit information and, in turn, this may lead to conflicts with sometimes long-lasting and disruptive social and political effects (Harrison *et al.*, 2019b). Examples of such divergent conclusions can be found with most hatchery supplementation operations and are well illustrated in Scotland, where managers have come to differing conclusions as to the efficacy of hatchery programmes in geographically and ecologically similar rivers, with, for example, the River Spey deciding to "fully embrace its hatchery operation" (Spey Fishery Board, 2019) despite evidence of marginal if any benefit to the fishery (Coulson *et al.*, 2013), whereas the River Dee concluded that "stocking of the Dee is not appropriate" (McDermott *et al.*, 2016).

Hatchery supplementation raises strong positions on both sides of the debate and this was recently well illustrated during the review and subsequent prohibition of stocking in Wales (Natural Resources Wales, 2014). Strong and entrenched divisions were seen on the pro- and anti-hatchery sides of the discussion, with an often lesser-heard compromise grouping being less vocal. The antagonistic groups disagreed on the effectiveness of stocking, the status of the salmon stock, had different management goals, and the debate was characterised by complex, intertwined and partly opposing beliefs and values (Harrison *et al.*, 2019b). The outcome of the consultation process was a prohibition on stocking in Wales (apart from some limited research) and, hence, a win/lose scenario for the different factions and an associated entrenchment of divisions.

In order to avoid, or at least mitigate, such antagonism, it is vital that the validity of different beliefs, values, objectives and goals are recognised during any cost/benefit evaluation (Redpath *et al.*, 2013). Decision-making should be collaborative (Harrison *et al.*, 2019b), where different stakeholder groups, including scientists and managers, work together to obtain evidence that is mutually accepted (Fujitani *et al.*, 2017; Harrison *et al.*, 2018a). Regulatory bodies can also assist in such a process by developing regulations that, where possible, avoid the necessity to enact a binary choice to either leave open or terminate stocking programs and where alternative approaches which achieve multiple and shared collaborative objectives, may be possible (Harrison *et al.*, 2019b). Thus, when evaluating the cost/benefit of any programme or regulatory framework, it is vital that collaborative strategies are developed that allow competing stakeholder groups to work toward shared realities and achieve multiple objectives (Harrison *et al.*, 2018b) to mitigate or avoid future conflicts (Harrison *et al.*, 2019b).

6. Plan

In order to both reduce/eliminate negative ecological impacts and maximise the ability to meet conservation objectives, it is vital that a management plan is developed in support of each stocking proposal. This formal plan should cover the rational, objectives, operation, monitoring and cost/benefit of the intervention. Although historically there has been large resource-investment in stocking activities, weaknesses in the success of many schemes appears to be the result of indiscriminate stocking without well-defined objectives or prior appraisal of the likelihood of success (Cowx *et al.*, 2012). Development of a detailed plan allows the various aspects of the intervention to be examined and the likelihood of achieving goals evaluated.

Management plan requirements vary depending on the regulatory requirements under which the activities are to take place. Hatchery interventions associated with US Pacific salmonids under the Endangered Species Act (ESA), for example, produce a standardised Hatchery and Genetics Management Plan (HGMP) (NOAA, 2020) which is used by the National Oceanic and Atmospheric Administration (NOAA) to evaluate impacts under the act. In contrast, in Canada, there is no federal policy that guides stocking and enhancement activities for Atlantic salmon, although some provincial governments have developed policies, and stocking activities by governmental and non-governmental organizations (NGO) are reviewed by defined oversight committees (NASCO, 2017a). In France, stocking is financed by the French government, with the support of local and regional authorities and based on a Migratory Fish Management Plan (plan de gestion des poissons migrateurs, PLAGEPOMI) for each major river basin (NASCO, 2017b). The Norwegian Environment Agency is the main regulatory authority in that country and The Norwegian Food Safety Authority and the Norwegian Water Resources and Energy Directorate also regulate hatcheries (NASCO, 2017c). There, stocking must be based on an approved plan, specific to the river concerned (Chaput *et al.*, 2017). In England, stocking regulation comes under the auspices of the Environment Agency (EA) and all stocking is expertly assessed on a case-by-case basis to determine if it meets the various criteria set out in the EA’s best practice and guidance documentation (NASCO, 2009). In Wales, stocking has been prohibited (Natural Resources Wales, 2014).

In Scotland, stocking programmes are regulated and authorised by various bodies under several legislative acts. Collection of wild broodstock in the close season is regulated by Marine Scotland acting on behalf of Scottish Ministers with hatchery operations controlled to some extent via fish health legislation. However, associated stocking of Atlantic salmon and sea trout is authorised directly by Non-Governmental bodies known as District Salmon Fishery Boards (DSFB) where these exist. In areas with no DSFB and for all other freshwater fish species, Marine Scotland regulates stocking, with detailed proposals from fishery operators being assessed on a case-by-case basis against the requirements of the Scottish Government stocking policy. DSFBs have their own individual criteria for assessment. Scottish Natural Heritage SNH (an agency of the Scottish Government) has a lead licensing responsibility for any proposed introduction of a species outside their native range, for example salmon stocking above an impassable natural barrier. Post authorisation, management and implementation of stocking is then carried out by DSFB's and/or fishery owners/operators.

Notwithstanding the variation in regulation among different countries, in many areas a general commonality in approach is the development of a science-based plan covering all the various aspects related to stocking, as outlined above, followed by expert evaluation through the lifetime of the proposed programme. In order that all aspects of the programme are covered, standardised planning documentation provides the best chance of capturing the various information required to make informed decisions. A particularly well-developed example of such an approach is the HGMP approach used in Pacific salmonid stocking. Numerous plans have been produced for individual supplementation schemes and are available to both NOAA and to the public for comment (template and guidance on NOAA, 2019).

7. Oversight

Plan development, hatchery operations, stocking activities and monitoring programmes are subject to the oversight of the various statutory regulatory bodies acting at both local and national levels. Programmes will thus be required to meet the requirements set out by such organisations. However, the successful implementation of supplementation programmes to meet both conservation and socioeconomic goals will be enhanced if oversight of the project is performed by a body consisting of representatives of the various stakeholder organisations involved (Harrison *et al.*, 2019b). Oversight should be science-led, with impartial experts examining the evidence to ensure progress is matching expectations, as outlined in the project plan, with appropriate cost/benefit/risk analysis carried out throughout the duration of the project (Cowx *et al.*, 2012).

8. Conclusions

In consideration of this scientific consensus, regulatory bodies are re-examining their stocking policies, leading in some regions to complete prohibition (e.g. Wales: Natural Resources Wales, 2014; Uttley, 2014). In other jurisdictions, however, different conclusions have been reached and stocking is still widely undertaken (Aas *et al.*, 2018).

There would seem to be a number of reasons for continuation of stocking in the face of the available scientific evidence. It may be, after careful consideration and investigation of all options, that stocking is determined to be a useful tool to be employed to fulfil a specific management objective. There are indeed a number of scenarios where stocking has been or is being rationally and successfully utilised in this way (ICES, 2017). In contrast, stocking is also being undertaken which is based not on scientifically rational management strategies but instead is driven by socio-political factors influenced to differing degrees by governmental agencies, local managers, commercial pressures, anglers, NGOs and other stakeholders (Young, 2017). Importantly among these drivers is the fact that, after considerable investment in hatchery infrastructure, it is difficult to reverse historic practices, especially when, in the absence of an understanding of the scientific consensus, it would seem, on the surface, that adding fish to a river is 'obviously' beneficial. Such well-intentioned interventions, carried out by people with a deep commitment to the well-being of their river systems, support an entire complex of management strategies and associated employment opportunities (Trushenski *et al.*, 2018). As such, there is considerable sociopolitical inertia supporting the maintenance of these strategies despite the often lack of evidence of their potential benefit and lack of harm they bring to the system/s.

In these times of declining salmon numbers, there is often understandable and significant societal pressure to attempt to reverse such trends and the establishment of a hatchery and associated stocking can often be seen by stakeholders as a both visual and positive step. However, hatchery supplementation programmes are resource intensive, difficult to monitor, and carry well-established potential risks to both wild populations of the stocked species and to the wider ecosystem. Nevertheless, they can also, in certain circumstances, potentially provide a useful and, in some cases, the only tool to mitigate environmental disturbances and conserve or enhance natural populations. Each particular programme will have its own set of drivers and ecological constraints, so determination of where it is likely to fall along the continuum of potential positive and negative impacts must be evaluated on a case-by-case basis. Such evaluation must be science-based but also include wider socioeconomic impacts, together with local, national and international advisory and regulatory factors. These various factors should be considered and addressed during the development of a comprehensive project plan.

Decades of research supports a simple evidence-based scientific consensus (Young, 2017): if the integrity of wild salmon is a management priority, stocking hatchery fish should be avoided where possible (Hilborn, 1992; Blanchet *et al.*, 2008;

Araki and Schmid, 2010; Palmé *et al.*, 2012). The genetic changes and loss of wild fitness, which has been well established in hatchery fish, place a significant risk to wild populations as such fish are released into systems. Competitive interaction with wild conspecifics at different life stages, together with impacts on the wider ecosystem may also negatively impact both the species of focus and the wider ecology of the river. Further, resources spent on potentially negative or ineffectual stocking might be better spent on other conservation strategies within the catchments. Such outcomes mean that, although as outlined above, in some situation's hatchery stocking may be an effective tool, depending on the objectives and circumstances (Arlinghaus, 2006; Lorenzen *et al.*, 2013; Camp *et al.*, 2014; Lorenzen, 2014; Arlinghaus *et al.*, 2016; Amoroso *et al.*, 2017; Johnston *et al.*, 2018), in many cases extreme care should be taken in order to avoid negative outcomes.

Recent reviews of stocking programmes showed that successful programmes addressed all stressors acting on the population, in contrast to many unsuccessful ones where not all stressors were, or could be, addressed (Araki and Schmid, 2010; ICES, 2017). These outcomes are well illustrated by the differing outcomes of the live gene bank programmes in the Bay of Fundy and Norwegian rivers. The Inner Bay of Fundy programme has been operating for more than 15 years, yet there is little evidence of progress towards the stated goal of the re-establishment of self-sustaining wild populations in the face of continuing stressor pressures (Fisheries and Oceans Canada, 2018). In contrast, the Norwegian gene banking programme has successfully re-established self-sustaining wild populations in more than ten rivers following removal of stressors, which, in this case, were either controlling acidity (Hesthagen and Larsen, 2003) or the complete removal of the *G. salaris* parasite (Norwegian Envornment Agency, 2020). The removal of stressors is thus seen to be of paramount importance to the outcome of a restorative stocking programme. Indeed, in the absence of stressor removal, there is not only the danger of the programme failing in its aims, but it might actually result in negative outcomes (Araki and Schmid, 2010) and act as a further stressor on the already threatened population (ICES, 2017).

As is the case with all stocking programmes, together with removal of stressors, outcomes rely on following a set of well-defined design steps. Historically, however, such steps have not been followed and this has meant that a rigorous evaluation of the effectiveness of such schemes is often extremely difficult, if not impossible (ICES, 2017; Glover *et al.*, 2018). Indeed, due to the fact that stocking has been such a widely used tool, it is impossible, in many cases, to single out the effect of the stocking versus the effects of other conservation measures and natural ecosystem changes which may be acting in parallel (e.g. Milner *et al.*, 2004; Griffiths *et al.*, 2011; ICES, 2017). Further, without such a rigorous evaluation, there is a risk of overestimating the stocking benefit whilst underestimating the role of alternative parallel restorative approaches, leading to an associated perpetuation of an inefficient restoration action which may inflict more harm than good (Carr *et al.*, 2015).

Following a precautionary approach means that appropriate risk assessment methodology should be developed and applied during programme development and before stocking commences. This would include the provision of all information necessary to demonstrate that a proposed stocking activity will not have a significant adverse impact on wild salmon populations or have an unacceptable impact on the ecosystem (NASCO, 2007). This same precautionary approach can also be used at the regulatory policy development level, where the costs/benefits/risks of the different types of supplementation programmes can be evaluated at both the scientific and socioeconomic levels. This principle is especially relevant for rivers which have enhanced protective status due to their particular conservation importance. However, every situation is different, and so in some situations, where the threat of extinction can be identified and is imminent and extreme, hatchery supplementation may provide a vital tool in the right circumstances as long as careful consideration is given to the inherent risks of such an approach.

All stakeholders have the same basic goals for their rivers and fisheries: to develop the means to help species maintain, recover or enhance their populations. Hatchery supplementation can play a part in such endeavours but may be the right or wrong tool, depending on the situation. It is thus vital that stakeholders come together to jointly work toward defining and achieving their common goals.

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Appendix 1

Reference list for risks and impacts associated with stocking (detailed in Table 1).

Issue	References
Hatchery	
Broodstock collection	(Ryman and Ståhl, 1980; Ryman, 1981; Utter *et al.*, 1989; Unwin and Glova, 1997; Wedekind, 2002; Was and Wenne, 2003; Vasemagi *et al.*, 2005; Williamson and May, 2005; Aho *et al.*, 2006; Neff *et al.*, 2008; Christie *et al.*, 2012b; Anderson *et al.*, 2013; Tillotson *et al.*, 2019; Östergren *et al.*, 2021)
Use of non-native stocks	(Garcia de Leaniz and Verspoor, 1989; Fritzner *et al.*, 2001; Ruzzante *et al.*, 2001; Schroeder *et al.*, 2001; Garcia de Leaniz *et al.*, 2007)
Domestication	(Swain and Riddell, 1990; Largiadèr and Scholl, 1995; Ryman *et al.*, 1995; Johnsson *et al.*, 1996; Fleming and Einum, 1997; Waples, 1999; Lynch and O'Hely, 2001; Sundström and Johnsson, 2001; Ford, 2002; Kostow *et al.*, 2003; Berejikian and Ford, 2004; Glover *et al.*, 2004; Araki *et al.*, 2007; Araki *et al.*, 2008; Blanchet *et al.*, 2008; Chittenden *et al.*, 2008; Frankham, 2008; Fraser, 2008; Araki *et al.*, 2009; Araki and Schmid, 2010; Chittenden *et al.*, 2010; Thériault *et al.*, 2010; Henderson and Letcher, 2011; Thériault *et al.*, 2011; Christie *et al.*, 2012a; Milot *et al.*, 2013; Christie *et al.*, 2014; Evans *et al.*, 2014; Zimmerman *et al.*, 2015; Berejikian *et al.*, 2016; Christie *et al.*, 2016; Berejikian and Van Doornik, 2018; Pinter *et al.*, 2019; Tillotson *et al.*, 2019)
Introduction of escaped farmed fish into broodstock	(Gausen, 1988; Thorpe and Stradmeyer, 1995; Glover *et al.*, 2017; Castellani *et al.*, 2018; Skaala *et al.*, 2019; Glover *et al.*, 2020)
Hatchery adaptation	(Le Luyer *et al.*, 2017; Rodriguez Barreto *et al.*, 2019)
Hatchery conditioning	(Vincent, 1960; Norman, 1987; McDonald *et al.*, 1998; Berejikian *et al.*, 2000; Metcalfe *et al.*, 2003; Kostow, 2004; McGinnity *et al.*, 2004; Jonsson and Jonsson, 2006; Blanchet *et al.*, 2008; Hawkins *et al.*, 2008; Chittenden *et al.*, 2010; Kallio-Nyberg *et al.*, 2011; Berejikian *et al.*, 2016)

Loss of resilience	(Araki *et al.*, 2008; McGinnity *et al.*, 2009; Sgrò *et al.*, 2011; Tillotson *et al.*, 2019)
Environmental	
Competition	(Wahl *et al.*, 1995; Beamish *et al.*, 1997; Pearsons and Hopley, 1999; Hilborn and Eggers, 2000; Levin *et al.*, 2001; Vasemägi *et al.*, 2001; Kostow *et al.*, 2003; Amoroso *et al.*, 2017)
Displacement	(Altukhov, 1981; Hindar *et al.*, 1991; Galbreath *et al.*, 2001; Marzano *et al.*, 2003)
Hybridisation (hatchery/wild)	(Hindar *et al.*, 1991; Waples, 1991; Busack, 1995; Campton, 1995; Leary, 1995; Skaala *et al.*, 1996; García-Marín *et al.*, 1998; Cagigas *et al.*, 1999; Machordom *et al.*, 1999; Palm and Ryman, 1999; Machordom *et al.*, 2000; Hansen *et al.*, 2001; King *et al.*, 2001; Mezzera and Largiadèr, 2001a; Mezzera and Largiadèr, 2001b; Marzano *et al.*, 2003; Araki *et al.*, 2009; Jasper *et al.*, 2013)
Hybridisation (inter-species)	(Verspoor, 1988; Garcia de Leaniz and Verspoor, 1989; Leary, 1995)
Immunocompromisation	(Currens *et al.*, 1997)
Enhanced straying	(Jonsson *et al.*, 1991a; Quinn, 1993; Cagigas *et al.*, 1999; Jonsson *et al.*, 2003; Clarke *et al.*, 2011; Brenner *et al.*, 2012; Keefer and Caudill, 2014)
Enhanced predation	(Kennedy and Greek, 1988; Collis *et al.*, 1995; Johnsson *et al.*, 1996; Shively *et al.*, 1996; Pearsons and Hopley, 1999; Walter *et al.*, 2005; Henderson and Letcher, 2011)
Introduction of parasites/pathogens	(Johnsen and Jensen, 1986; Elliott *et al.*, 1997)
Anthropological	
Overharvest	(Wright, 1981; Hilborn, 1985; Hindar *et al.*, 1991; Laikre and Ryman, 1996; Beamish *et al.*, 1997; Unwin and Glova, 1997)
Sociological impacts	(White *et al.*, 1995; Holling and Meffe, 1996; Burton and Tegner, 2000; Landres *et al.*, 2001; Holmlund and Hammer, 2004)

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