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Restoration and Enhancement of Salmonid Populations and Habitats with Special Reference to Atlantic Salmon

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Abstract.—Populations of Atlantic salmon *Salmo salar* can be restored and enhanced through planting of green or eyed eggs (embryos) in rivers and by releasing fry, parr, smolts, or postsmolts. The success of the releases varies with time and site of release, broodstock origin, size and age of the fish, and rearing and release techniques applied. However, egg, fry or parr releases cannot be used for augmenting populations above the carrying capacity of the water course. To surpass the carrying capacity, the fish should be released as smolts or postsmolts. Smolts released in rivers during spring migrate to sea for feeding but return to the river of release for spawning. Atlantic salmon released at the postsmolt stage may return to the release site when adult, but thereafter, they may stray to any of a number of rivers for spawning. As a result of ecological interactions, released juvenile hatchery fish may partly displace, increase the mortality, and decrease the growth rate, adult size, reproductive output, biomass, and production of wild conspecifics through density-dependent mechanisms working in freshwater. Hatchery-reared Atlantic salmon is usually competitively inferior to wild conspecifics both during feeding and spawning in rivers, due to environmental impacts and genetic changes that occur during the juvenile rearing. Habitat restoration is preferred when restoring endangered, threatened, or weak populations. Degraded spawning habitats can be reconstructed, and poor freshwater quality can be mitigated. In regulated rivers, rapid fluctuations in water level should be avoided, and the migratory activity of the fish can be stimulated by increased water flow. Populations can also be enhanced by expanding the accessible nursery habitat by use of artificial fishways through human induced or natural migration hindrances. Adaptive management practice is useful when restoring and rehabilitating populations and habitats. More knowledge is needed about environmental and genetic influences on the phenotype of hatchery fish and how habitats constrain salmon production in rivers.

Introduction

Restoration ecology, or the study of renewing degraded, damaged, or destroyed ecosystems and populations, is a rapidly growing field, stimulated by new knowledge about population and community ecology, behavioral ecology, genetics, and evolution (Jordon III et al. 1999; Van Andel and Aronson 2005). With the advancement of modern technology, the human ability to destroy habitats and use and overexploit populations have escalated at the same time as the awareness of our dependence of and responsibility for intact ecosystems have matured. Thus, researchers and laymen are searching for indicators of unspoiled ecosystems, and Atlantic salmon *Salmo salar* has become a symbol of clean, healthy aquatic ecosystems (Mills 1989).

Atlantic salmon forms anadromous populations. It spawns in freshwater. The offspring rear in rivers and lakes for 1–6 years before they migrate to sea as smolts, 10–30 cm in length. The postsmolts feed in the ocean for 1–4 years before attaining maturity and returning to their river of origin for spawning. An individual river may support one or more Atlantic salmon populations (Garcia de Leaniz et al. 2007).

Atlantic salmon is a very popular sporting species, and it is recognized as a delicacy. Therefore, the fishing pressure is high. The juvenile production in freshwater is recognized as the main limiting factor

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for the production of wild Atlantic salmon (Jonsson et al. 1998). Therefore, to increase the catch, populations have been enhanced by hatcheries for more than 150 years (Jonsson and Fleming 1993). In parallel with this activity, the salmon catch in the North Atlantic increased to a maximum in the mid-1970s. Since then, the catch has declined. This may be partly a result of reduced smolt production (Klemetsen et al. 2003; Jonsson and Jonsson 2004a; Quinn et al. 2006).

In freshwater, habitat destruction and alterations and introductions of exotic organisms have decimated salmon populations. For instance, acidification of Norwegian rivers has eradicated the Atlantic salmon in 25 water courses during the past century (Hesthagen and Hansen 1991). The monogene parasite Gyrodactylus salaries, accidentally introduced to Norway from the Baltic in the early 1970s, has since then decimated the juvenile Atlantic salmon production by between 80% and 90% in another 45 Norwegian rivers (Johnsen and Jensen 1991). These losses represent a reduction of about 50% in the Norwegian production of wild Atlantic salmon smolts (Hesthagen and Hansen 1991). Since the 1970s, the farming of Atlantic salmon has increased gradually and, with that, the escapement of fish from fish farms. The escapees may impact the wild Atlantic salmon populations negatively through ecological interactions, genetic introgressions, and the spreading of contagious diseases (Johnsen and Jensen 1994; Fleming et al. 2000; McGinnity et al. 2003; Jonsson and Jonsson 2006). Movements of hatchery fish between regions also increase the potential for the spreading of diseases such as furunculosis and proliferative kidney disease, killing salmon in the wild (Johnsen and Jensen 1994; Tops et al. 2006). Table 1 summarizes effects of hatchery salmon on wild conspecifics.

Survival and growth of Atlantic salmon at sea have also decreased with the growth of the salmon farming industry, and the abundances of marine parasites such as sea lice *Lepeophtheirus salmonis* and *Caligus* spp. have increased, with harmful effects on salmonids at sea (Heuch et al. 2005; Skilbrei and Wennevik 2006; Hvidsten et al. 2007). The decline in Atlantic salmon production since 1980 may be also related to climate change with warmer water (Friedland et al. 2000, 2005) and decreased food abundance at moderate latitudes (Beaugrand and Reid 2003; Kallio-Nyberg et al. 2006). With warmer climate, the annual growth rate of Atlantic salmon in freshwater has increased with reduced age and size at smolting as a consequence (Jonsson et al. 2005). Small fish are generally more vulnerable to predation at sea than larger conspecifics (Sundström et al. 2007). The abundances of some crustaceans in the northeast Atlantic have decreased since the 1980s, possibly with trophic effects mediated through the food chain, resulting in reduced marine salmon production (Helle and Pennington 1999; Beaugrand and Reid 2003). At least part of the Atlantic salmon population appears to feed farther north and in colder water than they did recently, resulting in slower growth (Jonsson and Jonsson 2004b). Fishing also reduces stock abundances, but it appears not to have contributed significantly to the recent stock decline in Atlantic salmon (Dempson et al. 2004). At present, the abundance of wild Atlantic salmon is low, and stock enhancements are very popular (Potter and Crozier 2000; Klemetsen et al. 2003). In the Pacific, coho salmon Oncorhynchus kisutch and Chinook salmon O. tshawytscha have undergone parallel decreases during the same period, probably for some of the same or similar reasons as Atlantic salmon (Noakes et al. 2000; Mote et al. 2003; Beamish et al. 2004b).

Here, we review common methods for restoring, rehabilitating, and enhancing Atlantic salmon populations and habitats. In particular, we focus on supportive breeding and effects of fish releases. During a long period, this has been the chief method for augmenting Atlantic salmon stocks. Furthermore, we discuss impacts of released hatchery salmon on wild populations and reasons why the success of hatchery fish often deviates from that of wild conspecifics. Then, we review possibilities for restoring and improving the Atlantic salmon habitat by various methods. We sum up by discussing the trade-off between restoring or stocking rivers and how adaptive management can be useful in this context and present some important research directions.

Population Restoration and Enhancement

Supportive Breeding

Supportive breeding involves the gathering of gametes artificially stripped and fertilized. The resulting progeny are reared in hatcheries and released at vari-

Table 1.—Effects of released hatchery-reared fish on wild populations.

Classes of interactions	Responses	Sources
Ecological competition	Parr emigration from river stretches at high fish densities.	McMichael et al. 1999, 2000; McGinnity et al. 2003; Weber and Fausch 2003
	Parr mortality at high fish densities.	Nickelson et al. 1986; Vincent 1987; Nielsen 1994; McGinnety et al. 1997, 2003
	Reduced growth at moderate fish densities.	Bohlin et al. 2002; Imre et al. 2005
Genetic interbreeding	Reduced reproductive success, offspring survival and production.	Fleming et al. 1996, 1997, 2000; McGinnity et al. 1997, 2003, 2004
Spreading of diseases and parasites	Furunculosis (*Aeromonas salmonicida*).	Johnsen and Jensen 1994; Glover et al. 2006
	Gyrodactylosis (*Gyrodactylus salaries*).	Johnsen and Jensen 1994; Bakke and Harris 1998; Peeler et al. 2006.
	Salmon lice (*Lepeophtheirus salmonis* and *Caligus* spp.).	McVicar 2004; Heuch et al. 2005; Hvidsten et al. 2007
	Proliferative kidney disease (*Tetracatculoides bryosalmonae*)	Tops et al. 2006

ous life stages (i.e., eggs, fry, older parr, smolts, or postsmolts). Releases of eggs or unfed fry (alevins) are often used where environmental conditions during spawning limit recruitment. If nursery areas limit population size, such as in many rivers regulated for hydropower purposes, releases of older juveniles may be more suitable. Economic costs of these release practices vary directly with the length of the hatchery rearing required. However, since juvenile survival in freshwater increases with the length of the hatchery rearing, this may at least partly compensate for the additional rearing costs.

Hatcheries are important tools in the supplementation and enhancement of yields for fisheries. Sea ranching operations, involving the release of hatchery juveniles, which return to the point of release as adults, are used to support recreational and professional fisheries. Supportive breeding is used in many rivers regulated for hydropower production where dams isolate the fish from upstream spawning grounds or water is channeled away from the river. Hatchery methods and technology have been much improved during recent years in parallel with the growth of the salmon farming industry, and massive development of hatchery programs for the above purposes has resulted in Atlantic salmon becoming one of the most intensely, artificially supplemented organisms in the world.

Why Are Fish Released?

There are periods in the life cycle of salmon with marked reductions in abundance because of population bottlenecks. Fish are released to escape the effect of such bottlenecks. Positive effects of stocking can be achieved if natural reproduction in the river is below its carrying capacity, if Atlantic salmon are released in habitats above the natural salmon producing stretches of rivers or in rivers where the spawning but not the juvenile rearing habitat is degraded.

Periods of high mortality occur when there is a marked ontogenetic shift in diet or habitat. Examples of such changes in diet are yolk to first feeding on small drifting invertebrates and then a diet change from invertebrates to fish. Examples of habitat change with fish age are open water in riffles to deeper pools in streams, pools in tributaries to the larger parent river, river to estuary, estuary to ocean, ocean to freshwater of the parent river, and river to spawning ground in the natal stream (Elliott 2001).

The resource limitation will affect the life stage most dependent on the resource, and a population bottleneck will occur. The chief bottlenecks occur in the early life stages such as the times of first feeding and smolting (Gibson 1993), although there may sometimes be population regulation later in life as well (Weatherley and Gill 1987; Shuter 1990). The bottlenecks may affect released hatchery fish as well as the local population. According to Sægrov et al. (2001), water discharge is a major factor influencing the carrying capacity of Atlantic salmonid parr. Based on studies from 11 rivers in western Norway, they found that the carrying capacity was inversely related to the natural logarithm of the water discharge between 2 and 70 m^3/s. Factors associated with high discharge constrain the parr production, especially during early summer when high water velocity restricts the area of available habitat.

Although the carrying capacity for salmon parr in a river changes from year to year, rivers can be characterized by an average carrying capacity with fluctuations around this average. The carrying capacity is largely determined by the variations in the physical and chemical conditions, the frequency of extreme events such as droughts and spates, the availability of food, and the density of other fish species and the density of different life stages of the same species (Elliott 2001). Thus, carrying capacity reflects the effect of all the environmental variables and density-dependent factors and sets the long-term maximum level of population density. As the population size approaches the carrying capacity of the area, emigration and mortality will increase (Einum and Nislow 2005). After that regulatory phase, mortality is influenced mainly by density-independent factors (Jonsson et al. 1998; Milner et al. 2003; Su et al. 2004), although exceptions exist where density-dependent mortality occurs at a later stage (Unwin 1997; Elliott and Hurley 1998). Thus, salmon rivers can be stocked to fill the available niches for salmon, and populations can be enhanced by releasing fish after the main periods of population regulation.

Salmon Stocking

Egg Planting

Salmon eggs (embryos) are placed in incubating boxes buried in the gravel bed of rivers or freely in the bottom substratum, imitating a natural salmon redd (Barlaup and Moen 2001; Johnson 2004). Newly fertilized eggs and eyed eggs are the two developmental stages usually used. (1) Newly fertilized eggs (green eggs) are planted between 24 and 48 h after the fertilization and water hardening. After that (but before the eye stage), the eggs are very sensitive to handling stress and easily killed if moved. (2) Eyed eggs are robust and tolerate substantial handling and are often used for planting (Wagner et al. 2006). The survival of planted eggs is variable (Table 2), and there is no systematic difference in survival between eggs planted in boxes or placed directly in the gravel substratum or whether they are buried as green or eyed eggs. The survival from fertilization to hatching is similar for the two methods (Kelly-Quinn et al. 1993). However, planting of eyed eggs is often preferred since this allows for proper veterinary health control of the spawners before the eggs are planted. Furthermore, when using eyed eggs, there is a less strict time constraint on the planting. Since newly fertilized eggs are very sensitive to movement after 48 h, movements of the substratum during freshets or spates may kill the eggs.

When eggs are planted directly into the gravel substratum, they are usually placed in areas where the salmon spawn. The selection of the site is critical to the survival of the eggs. Preferred spawning areas have variable particle size, and the nests have a few

Table 2.—Survival (%) of various developmental stages of hatchery-reared Atlantic salmon.

Stocked stage	Survival to	Survival %	References
Eggs	hatching	0–100	Reviewed in Barlaup and Moen 2001
Eggs	emergence	3.3–89	Reviewed in Barlaup and Moen 2001
Unfed fry	smolts	0.2–15	Rosseland 1975; reviewed in Fjellheim and Johnsen 2001
Fry	adults	0.7–5.9	Berg 1969; Hansen 1991
Smolts	adults	0–11.6	Reviewed in Finstad and Jonsson 2001

large stones in the centre of the egg pocket. These stones stabilize the redd and give a sheltered environment for the eggs. Usually, Atlantic salmon spawn between 500 and 1,000 eggs in each nest (Fleming 1996). The median particle size of the gravel substratum where salmon spawn is about 10% of their body length (Kondolf et al. 1993), and the eggs are often buried at 10–30 cm depth in the substratum, the deeper the larger the fish is (DeVries 1997). When mimicking natural redds, the egg pocket is covered by gravel washed free of fine sediment to allow proper oxygenation of the eggs. The survival of the eggs depends on the permeability of the gravel (Kondou et al. 2001), and there is negative correlation between the dissolved oxygen concentration and the mortality rate of the eggs (Malcolm et al. 2003). Furthermore, embryos developing at low dissolved oxygen concentrations are smaller at hatching than those developing under more favorable conditions (Youngson et al. 2004).

More commonly than planting eggs in artificial redds, they are planted in boxes or trays buried in the gravel substratum. Common devices are the Whitlock-Vibert box (Vibert 1949; Whitlock 1978), various types of perforated plastic boxes (Harris 1973; Scrivener 1988; Rubin 1995), and plastic trays (Raddum and Fjellheim 1995; Donaghy and Verspoor 2000). Common problems are a too high egg density in the boxes and that the eggs cluster together and become susceptible to bacterial and fungal infections, oxygen deficiencies, and sedimentation of fine-particulate material (Harshberger and Porter 1979; Chapman 1988; Scrivener 1988; Tabachek et al. 1993).

Under favorable conditions and properly done, the hatching success of planted eggs exceeds 90% (Humpesch 1985; Kelly-Quinn et al. 1993). A key to success is to provide suitable conditions such as proper gravel composition, burial depth, number of eggs per pocket, and hydrological conditions (Barlaup and Moen 2001). In most cases, egg plantings are more cost-effective than rearing and releasing hatchery fry, parr, or smolts. On the other hand, the survival is higher if the fish are released at a more developed stage (Coghlan and Ringler 2004; Johnson 2004).

Fry and Parr Stocking

Stocking of young salmon in rivers and lakes is a useful method if the habitat is spawning-site limited (Hyatt et al. 2005). Cultivation of Atlantic salmon commenced with the building of the first hatcheries in the 1850s. Initially, the fish were stocked as alevins and small fry, but older fish were released as the rearing technique improved. The stocking efforts were further stimulated by declining populations due to regulations of rivers for hydropower production and the continued acidification of rivers in northern countries, which started about 1875 (Hesthagen and Hansen 1991). River-owners' organizations, fishing societies, and management agencies ran hatcheries to enhance the river production and yield for fisheries, for conservation purposes to save populations at risk of extinction, or to reestablish populations that had been eradicated (Jonsson et al. 1999; Fleming and Peterson 2001). Often, the results of such releases were not evaluated, and most of the evaluations reported tend to be among the more successful ones.

The published results of fry and parr stocking vary. Particularly high survival of unfed Atlantic salmon fry was reported from releases in a tributary to the River Sandvikselva, south Norway (Rosseland 1975). There was no anadromous fish present prior to the release. A stocking density of two unfed fry per square meter gave about 0.3 smolt/m^2 (Table 1). This was a very productive stream, and a similar stocking density gave less than 8% of this when tested in tributaries of the River Vefsna, northern Norway (Johnsen et al. 1997b). In the latter case, the survival from smolts to returning adults was estimated at 2%. Later releases gave even poorer survival with 0.85% as the mean for a subsequent 6-year release period (Johnsen et al. 1997a).

There are also examples of parr releases giving excellent survival to adults. Hansen (1991) reported 2.3% survival to returning adults of 14 000 one-summer-old parr released in 1983. The fish were liberated above the natural Atlantic salmon producing area of the River Drammen, south Norway. When repeating the experiment in 1986, the survival of 50 000 one-summer-old parr released in the same area was 0.7%. The lower yield of the repeated release may be because the food base was exploited by the earlier release of parr or that the carrying capacity of the freshwater habitat was surpassed because too many fish were released. Releases of Atlantic salmon in rivers appear particularly successful if there is no other fish species present (Fjellheim and Johnsen 2001), but even with the presence of nonanadromous populations of salmonids such as brook char *Salvelinus fontinalis*, brown trout *S. trutta*, and rainbow trout *O. mykiss*, the parr survival of Atlantic salmon can be high (MacCrimmon 1954; Egglishaw and Shackley 1980; Kennedy and Strange 1986; Whalen and LaBar 1998; Jokikokko 1999; Jutila et al. 2003).

An example of an unfortunate result is the parr releases from the West-Norwegian River Teigdalselva, a tributary to the River Vosso (Fjellheim and Johnsen 2001). In total, 70,000 1-year-old parr were released giving almost no smolts. In this river, a large part of the water was directed to a hydropower station outside the catchment area. The carrying capacity for Atlantic salmon smolts had obviously decreased dramatically as a result of the decreased flow.

The success of the releases is influenced by the quality, size, and density of the stocked fish and time and place of stocking (Connor et al. 2004; Saltveit 2006). Jokikokko (1999) reported that both point and scatter stockings are suitable methods for supplementing Atlantic salmon parr in rivers. Letcher and Terrick (2001) reported that a wide range of developmental stages of Atlantic salmon fry will survive equally well and grow to a similar size when released in a natural system. On the other hand, even a small difference in introduction site and time can influence the migratory behavior of the fish (Pirhonen et al. 2003) and have long-term effects on body size, survival, and life history expressions (Letcher et al. 2004). Jokikokko and Jutila (2004) found that stocking of 1-year-old parr was economically more cost-effective than stocking of one-summer-old parr when restoring endangered stocks. A less cost-effective way of enhancement is the release of 2-year-old parr (Salminen et al. 2007). Large size at release has a positive effect on survival as also reported for masu salmon *O. masou* (Miyakoshi et al. 2003), but the economic cost of rearing one extra year is high. Therefore, there must be a good reason for an extra year of parr rearing before releasing the fish, such as avoidance of an effective local parr predator.

The release site influences the recapture rate. In some cases, stockings of Atlantic salmon parr in lakes have been very successful (Berg 1969; Pedley and Jones 1978; Pepper et al. 1992). However, the flow through of many lakes is small, and Hansen (1987) reported that one-summer-old parr released in Lake Storevatnet of the River Imsa, southwest Norway moved downstream over an extended period, compared with wild smolts produced in the downstream river. He attributed this to the low flow-through making it difficult for the fish to find the lake outlet. It is also possible that the River Imsa salmon is a river population not adapted to navigate through lakes. The outlet river is their original habitat to which they have been adapted through several thousand years. Further research is needed to establish whether difficulties in finding the lake outlet are an attribute of the habitat or a population-specific adaptation found in some Atlantic salmon populations.

Removing broodstock from rivers for hatchery rearing and release from an already depleted spawning stock may result in even further population decline (Saltveit 1998). In spite of extensive stocking of parr in the River Suldalslågen, southwest Norway, there has been a steady decline of Atlantic salmon in the river, where a large part of the water is channeled from the main river to the sea. Although about 50% of the smolts that leave the river are of stocked origin, most returning adults are naturally produced. In spite of this, broodstock was taken from the reduced number of returnees, leaving even fewer fish for reproduction. On this basis, the stocking program was advised to be discontinued. Thus, the results in various stocking programs vary, and poor results are reported in inferior habitats. There is little reason for stocking salmon at densities way above the carrying capacity of a system (Brännäs et al. 2004) because the density-dependent response is reduced parr survival and growth of the local fish (Imre et al. 2005). To enhance depleted populations, one may sample the broodstock in an abundant population nearby where the environmental conditions are similar, as the removing of spawners can be detrimental to the stock. Natural spawning is superior to fry or parr stocking in rivers with intact breeding grounds, and the stocking success is generally low in rivers where the density of naturally bred conspecifics is high (Crozier et al. 1997; Verspoor and Garcia de Leaniz 1997; Mowbray and Locke 1998).

Smolt Release

The productivity and size of the freshwater habitat constrain the sizes of Atlantic salmon populations (Jonsson et al. 1998), and the release of hatchery-reared smolts have been used to augment Atlantic salmon populations since the first part of the 20th century. Smolts have been released to compensate for habitat loss due to dam and impoundment building of streams and use of water for hydropower production. However, if the habitat is intact, the release of 1-year-old parr appears more cost effective than smolt releases (Jokikokko et al. 2006).

Hatchery smolts start their seaward migration immediately after release (Hansen and Jonsson 1985; Jonsson and Fleming 1993), and many return to the place of release when sexually mature (Hansen et al. 1993). To enhance the spawning population of a river, the smolts should be released in the river. Fish released in river estuaries stray more to other rivers and are delayed in their upstream spawning migration compared with smolts released higher upstream (Jonsson et al. 1994; Insulander and Ragnarsson 2001). The smolts should be released in spring, at the time of seaward migration for wild smolts in the same or similar, neighboring rivers. Smolts released at that time survive better and stray less frequently than fish released at other times of the year (Hansen and Jonsson 1989a, 1991a).

The survival of released hatchery salmon is often low (Table 3), usually less than half of that of wild smolts (Jonsson et al. 1991, 2003b; Jutila et al. 2003). Commonly, the recaptures of the adults are in the range of 0.5–3.0% (Finstad and Jonsson 2001), although recapture rates above 11% have been observed (Hansen and Jonsson 1990; Hansen et al. 1997). According to Moksness et al. (1998), the recapture rates should be above 10% to be economically profitable in sea ranching operations, which is only rarely obtained (Finstad and Jonsson 2001). The reduced survival of hatchery smolts may be partly caused by the artificial rearing conditions resulting in decreased smolt quality and poor handling and release procedures. Furthermore, the released fish may not be genetically adapted to the system of release or have a too small genetic variability (Ayllon et al. 2004; McGinnity et al. 2004; Garcia de Leaniz et al. 2007).

The yields of the releases differ depending on smolt size and age. Hansen and Jonsson (1989b) reported that 2-year-old smolts gave higher yields than 1 year olds. The yield of the 2 year olds varied between 125 and 1,050 kg/1,000 smolts released. A similar difference caused by smolt age was reported from smolt releases in southern Finland (Salminen et al. 2007). On the other hand, it is cheaper to produce 1- than 2-year-old smolts, which can make it economically more profitable to produce 1- than 2-year-old smolts as recently found in Norway (Jonsson et al. 2003b). Among similar-aged fish, large individuals appear to survive better than smaller ones as reported for masu salmon in Japan (Miyakoshi et al. 2003) and pink salmon *O. gorbuscha* in Alaska (Moss et al. 2005).

A large number of experiments have been performed to increase the survival of released hatchery smolts, and effects of the rearing and release methods have been tested (Finstad and Jonsson 2001). For instance, handling, transport, and anesthesia stress anadromous salmonids (Nikinmaa et al. 1983; Hansen and Jonsson 1988; Barton 2000), and stress-related cortisol surges can suppress the immunological capacity (Fries 1986; Iversen et al. 1998) and migratory activity (Specker and Schreck 1980). But even when handling and transport are kept at a minimum and no hatchery smolt is anesthetized within 2 weeks of release (Pickering et al. 1982), the survival rate of hatchery reared smolts is between one and two times lower than that of comparable groups of wild smolts (Jonsson et al. 2003b).

Time and place of release have been optimized through experimental releases during the 1980s and 1990s (Hansen and Jonsson 1986, 1989a, 1991a; Hansen et al. 1989; Jonsson et al. 1994). Experiments have been performed to adapt the parr to natural food items or predator training before release, but none of these have so far been successful in improving the sea survival substantially. Increased water level during the emigration period has a positive effect on the smolt survival (Hvidsten and Hansen 1988). Futhermore, physical exercise of the parr has proven to be positive for survival and growth in hatcheries (Jørgensen and Jobling 1993; Davidson 1997). So far, however, exercised Atlantic salmon have not significantly improved return rates to the river of release, although exercised fish strayed less to other rivers than unexercised fish (Skilbrei and Holm 1998).

Hatcheries tend to produce elevated levels of sexually mature male parr, which more often become freshwater resident than what immature parr do (Hansen et al. 1989). To increase their emigration rates to the same levels as those of immature smolts, their high steroid concentration can be decreased either through gonadal stripping or elevated

Table 3.—Changes occurring in hatcheries reducing the performance of released hatchery fish in nature.

Changes in	Changed character	Sources
Morphology	Body form and size	Taylor 1986; Swain et al. 1991; Fleming et al. 1994; Fleming and Einum 1997; Fiske et al. 2005; Von Cramon-Taubadel et al. 2005
	Distored jaws	Fleming et al. 1994
	Fin damage	Höglund et al. 1997; Lellis and Barrows 1997; Ellis et al. 2002; Latremouille 2003
	Scale loss	MacLean et al. 2000; Lacroix and Knox 2005
	Adiposy	Rowe et al. 1991; Silverstein et al. 1999
Physiology and anadromy	Heart abnormity	Poppe et al. 2003; Seierstad et al. 2005
	Brain	Marchetti and Nevitt 2003; Lema et al. 2005
	Metabolic rate	Dunmall and Schreer 2003; Claireaux et al. 2005
	Smolting	Poole et al. 2003
	Hormone	Youngson and Webb 1992; McCormick et al. 2003
Life history characters	Growth rate	Jonsson et al. 1991a; Jonsson and Fleming 1993; Kistow 2004
	Survival	Piggins and Mills 1985; Jonsson and Fleming 1993; Jonsson et al. 1991a, 2003b; Kostow 2004; Saloniemi et al. 2004
	Smolt age	Økland et al. 1993; Yamamoto and Morita 2002; Jonsson et al. 2003b; Duston et al. 2005
	Age at maturity	Jonsson et al. 2003b; Kostow 2004; Patterson et al. 2004
	Reproductive output	Jonsson et al. 1996; Tamate and Maekawa 2000; Fleming et al. 2003; Quinn et al. 2004
	Longevity	Kostow 2004
Behaviour	Time of river ascent	Jonsson et al. 1990b, 1994; Fleming et al. 1997; Skilbrei and Holm 1998
	Risk taking	Berejikian 1995; Fleming et al. 2002; Sundström et al. 2004
	Feeding behavior	Reiriz et al. 1998; Reinhardt 2001; Sundström and Johnsson 2001; Brown et al. 2003a, 2003b
	Aggressive behavior	Einum and Fleming 1997; Rhodes and Quinn 1998; Riley et al. 2005; Sundström et al. 2003; Yamamoto and Reinhardt 2003
	River movement	Jonsson et al. 1990a; Økland et al. 1995
	River stay	Jonsson et al. 1990a
	Straying to foreign rivers	Hansen et al. 1993; Jonsson et al. 2003a
	Predator recognition	Brown and Smith 1998; Mirza and Chivers 2000; Berejikian et al. 2003b; Vilhunen et al. 2005
	Refuge use	Griffiths and Armstrong 2002; Orpwood et al. 2004
	Swimming activity	McDonald et al. 1998; Claireaux et al. 2005
	Spawning time	Berejikian et al. 2003a
	Courting and spawning behavior	Fleming et al. 1996, 1997

water temperature during the winter after maturation (Berglund et al. 1991). Vaccines and chemical protection against contagious diseases and parasites such as sea lice have a positive effect on the survival of hatchery smolts in nature (Hvidsten et al. 2007). But even sea lice-protected smolts exhibit inferior survival to adulthood. Thus, improved handling and release strategies can increase the survival of released hatchery smolts but have so far not brought the survival rate up to a satisfactory level (Jonsson et al. 2003b).

Postsmolt Release

Survival of released smolts can be increased by increasing the size of the fish at release (Salminen et al. 1995), and the mortality may be particularly high due to predation during the first weeks at sea (Hvidsten and Møkkelgjerd 1987; Salminen et al. 1995; Dieperink et al. 2002). To avoid coastal smolt predators, postsmolts have also been released directly in the ocean after transportation in well-boats (Gunnerød et al. 1988; Heggberget et al. 1991). Furthermore, postsmolts have been retained in sea pens a few weeks during the first summer after smolting and then released. Both methods have given significantly higher recapture rates compared with fish released in rivers at the time of smolting (Eriksson and Eriksson 1991). A similar effect has been reported from coho and Chinook salmon, although the results vary among stocks (Linley 2001; Thrower and Joyce 2006). However, coastal released Atlantic salmon have exhibited a temporal delay in river ascent relative to the river-released fish and exhibited higher straying rates to other rivers compared with river-released fish (Hansen and Jonsson 1991a; Hansen et al. 1993; Jonsson et al. 1994).

Effects of Hatchery Salmon on the Local Wild Fish

Juvenile Competition

The results from experimental tests of feeding competition between wild and hatchery Atlantic salmon vary. Einum and Fleming (1997) reported that parr of hatchery Atlantic salmon dominated wild conspecifics in one-on-one challenges, with hybrids exhibiting an intermediate success. They related this to higher aggressiveness in hatchery than wild fish. A similar dominance of hatchery fish was reported by Rhodes and Quinn (1998) for coho salmon. Berejikian et al. (1999) found that juvenile coho salmon with cultured mothers won dominance challenges in a laboratory flume more frequently than parental half-sibs with wild mothers, suggesting that dominance may be a maternal effect. Riley et al. (2005), on the other hand, found no evidence that rearing environments caused higher aggression in cultured than in wild steelhead (anadromous rainbow trout) fry.

The higher aggressiveness observed in some hatchery populations can be modified by the environment. Fleming and Einum (1997) reported that hatchery parr were more aggressive in tank environments, contrasting the dominance of wild juveniles in stream-like environments. In brown trout, Höjsjö et al. (2004) found that the growth rate of dominant individuals relative to subordinates decreased with increased habitat complexity lending support to the hypothesis that habitat complexity favors wild salmonids in competition with hatchery reared conspecifics.

Prior residence influences the outcome of competition between wild and hatchery-reared fish (Reinhardt et al. 2001). In Atlantic salmon, it influences which individuals obtain territories (Cutts et al. 1999). In brown trout territory, owners are more likely to win contests, whether the fish are of wild or cultured origin (Sundström et al. 2003). A prior residence of 4 d motivated a stronger defense than a 2-d resident (Johnsson and Forser 2002). Furthermore, levels of aggression in juvenile Atlantic salmon are lowered by the presence of larger individuals (Adams et al. 2000; Peery et al. 2004). Thus, although hatchery parr may win feeding contests in tanks with slowly flowing water, the dominance can be reversed if intrinsic or extrinsic conditions change. Competition may result in increased emigration and mortality and decreased individual growth through density dependent mechanisms.

Displacement and Mortality in Freshwater

In rivers, hatchery parr may be displaced by wild conspecifics and vice versa, as found in experiments with rainbow trout (Table 3). Whether or not cultured fish dominate over wild conspecifics vary with the genetic background of the fish (Weber and Fausch 2003). McGinnity et al. (1997) reported that cultured Atlantic salmon fry outgrew and partly replaced wild conspecifics. The possible displacement may be linked to body size and density of fish. Weiss and Schmutz (1999) observed movement of resident brown trout from stocked stream sections. There are also examples where no effect of hatchery parr has been observed. For instance, Orpwood et al. (2004) reported that the ability of wild Atlantic salmon parr to find shelter in winter was unaffected by the presence of hatchery parr, even when the wild fish were outnumbered by four to one. Nickelson et al. (1986) found that the density of wild coho salmon juveniles was lower in streams stocked with hatchery fish than in unstocked streams, indicating that cultured fish replaced wild fish. The total density of juveniles had increased 1 year after stocking, but there was decreased production of juveniles in the next generation.

Weber and Fausch (2003) reported that at high density, hatchery rainbow trout were able to displace wild conspecifics from favorable stream positions when the hatchery fish were larger. At normal density, however, no consistent effect on emigration was found. In any case, it may be wise to delay the release of hatchery fish until after smolting of the local fish in the river to reduce potential interactions in freshwater.

There is little evidence of mortality effects of hatchery-reared Atlantic salmon parr on wild conspecifics, but experimental evidence from a number of other salmonid species indicates that density dependent mortality can result from releases of hatchery parr. Nielsen (1994) reported reduced production of wild coho salmon after hatchery coho salmon were stocked in a Californian river. Vincent (1987) found that densities of wild rainbow trout and brown trout increased after the stocking of adult hatchery rainbow trout ceased in two Montana streams, and Petrosky and Bjornn (1988) found that the mortality of wild rainbow and cutthroat trout *O. clarkii* increased at high, but not low stocking densities. In competition experiments with masu salmon in river enclosures, the hatchery fish survived in larger numbers than wild fish (Reinhardt et al. 2001). The mortality effect of released hatchery fish may be similar to that of adding wild fish, as reported by Bohlin et al. (2002) who tested effects of competition from hatchery on wild brown trout. Thus, in freshwater, density-dependent effects of cultured fish appear common among salmonid species and is probably also taking place in Atlantic salmon.

Releases of hatchery salmon may increase the mortality of competing species. Levin and Williams (2002) reported that the survival of wild Chinook salmon was negatively associated with releases of hatchery-reared steelhead in the Snake River, western USA, and similarly, Atlantic salmon releases influence the carrying capacity for brown trout as a result of competitive interactions (Heggenes et al. 1999; Harwood et al. 2001; Armstrong et al. 2003; Höjsjö et al. 2005). However, the effect of interspecific competition will probably be smaller than that of intraspecific competition between hatchery and wild Atlantic salmon. Although the ecological requirements of various species may be similar, they are less similar than those of hatchery and wild conspecifics (Harwood et al. 2002).

Growth

Density can influence the growth rate of salmonids (Brännäs et al. 2004). While density dependent displacement occurs at high population densities, density-dependent growth reduction can be noticeable even at low population densities (growth depensation) (Jenkins et al. 1999; Lobon-Cervia 2005). In addition to Atlantic salmon (Imre et al. 2005), growth depensation caused by released hatchery fish has been observed in brown trout and rainbow trout, and it probably occurs among stream-living salmonids in general (McMichael et al. 1997, 2000; Weiss and Schmutz 1999; Sundström et al. 2004). Bohlin et al. (2002) found that the addition of hatchery trout had a similar effect on growth rate of wild brown trout as increasing the density of wild conspecifics. For Chinook salmon, Weber and Fausch (2005) reported an even stronger negative effect on wild fish growth by adding hatchery than adding wild fish to the same density. In addition, releases of hatchery fish may influence growth rate of competing species, as found in experiments with brown trout and cutthroat trout (Shemai et al. 2007). But the negative interspecific effect on growth rate may be less than the intraspecific effect. An indirect consequence of the growth depensation may be decreased survival rate and impacts on other life history traits of the fish (Beamish et al. 2004a; Jonsson and Jonsson 2004b).

Other Life History Traits

The presence of hatchery salmon can contribute to the decline in adult body size of the fish in localities where they are released due to feeding competition. Hatchery practices together with fast juvenile growth in freshwater often results in younger age at maturity, as a phenotypic response (Salminen 1997; Quinn et al. 2001; Bates and McKeown 2003; Vøllestad et al. 2004; Scheuerell 2005). Furthermore, selective broodstock selection may alter the age at maturity of the fish as found for Chinook salmon (Unwin and Glova 1997).

With a decrease in juvenile growth rate and adult body size, egg size and fecundity may be altered (Unwin and Glova 1997). In Atlantic salmon, fast juvenile growth rate in freshwater, such as in hatcheries, reduces egg size and increases the fecundity of the fish as a plastic response of the phenotype, whereas the effect on egg size of growth rate variation at sea is minimal (Jonsson et al. 1996), relationships that also hold for masu salmon (Tamate and Maekawa 2000). Variation in growth rate, adult size, age at maturity, egg size, and fecundity influence competitive ability, reproductive success, and fitness of the fish with effects on biomass and production of fish in nature (Wertheimer et al. 2004).

Sea Survival

Released hatchery salmon survive less well than wild salmon at sea. In the Burrishoole, Ireland, smolt-to-adult survival of one sea-winter Atlantic salmon averaged 8% (2.9–12.6%) for wild fish and 2% (0.4–4.4%) for sea-ranched fish (Piggins and Mills 1985). In the River Imsa, the mean sea survival during 14 years of study was 8.9% for wild and 3.3% and 2.9% for cultured fish released as 1- and 2- year-old smolts, respectively (Jonsson et al. 2003b). In the Baltic Sea, the smolt to adult survival was 4.5 times higher in wild than in released hatchery Atlantic salmon (Saloniemi et al. 2004). It was reported that the difference in sea survival was more pronounced in low-survival years than in high-survival years. In good years, the larger size of hatchery smolts could compensate for their inferior performance, compared with wild smolts, but in poor survival years, wild smolts always exhibited higher survival. The estimated mean survival from smolts to adults of naturally produced steelhead was 5–6%, whereas that of hatchery populations was approximately 1%, and total egg to adult survival was 0.05% for wild fish and 0.56% for cultured fish (Kostow 2004). The 3–5 times higher sea survival of wild than hatchery reared Atlantic salmon and steelhead trout released in rivers as smolts may be linked to more relaxed selection pressure in hatcheries than in nature and the phenotypic divergences of hatchery from wild fish (Jonsson and Fleming 1993; Reisenbichler and Rubin 1999; Ford 2002). Also, in other salmonids, the survival of released hatchery fish can be low as reported for released hatchery-reared anadromous brown trout in Denmark due to high mortality at sea (Hansen 2002; Ruzzante et al. 2004).

Spawning Competition and Reproductive Success

Returning adult hatchery Atlantic salmon enter rivers to spawn later in the season, move about more, and stay for a shorter time in the river than wild fish (Jonsson et al. 1990a; Økland et al. 1995). Upstream migrating hatchery salmon may not be heading for any particular spawning area. Many may move to the top of the river instead of entering the spawning grounds of wild fish lower downstream (Thorstad et al. 1998). Some released hatchery-reared Atlantic salmon spawn in the river they enter; others leave the river unspawned (Jonsson et al. 1990a). The spawning success of hatchery salmon may be reduced by their late river entry (Aarestrup et al. 2000).

On the spawning grounds, hatchery Atlantic salmon have been found competitively and reproductively inferior and injured more often than their wild counterparts (Jonsson et al. 1990a). Fleming et al. (1997) reported that the spawning success of male Atlantic salmon released as smolts was 51% of that of corresponding wild males from the same population, whereas there was no significant difference in reproductive success between wild and hatchery females. McGinnity et al. (2004) reported an overall lifetime success from fertilized egg to returning adult of nonnative Atlantic salmon to be 35% less than that of native and conspecifics released as smolts. Early survival was lower in offspring of hatchery than of wild fish; later, it was similar. Also, in other salmonids such as coho salmon, the reproductive success is higher for wild than for hatchery-produced fish (Fleming and Gross 1992, 1993; Berejikian et al. 1997).

The release of hatchery-reared adults is not an effective tool to rebuild a seriously depressed population (Carr et al. 2004). The reproductive success of hatchery fish, however, may increase with increasing time in nature. For instance, the reproductive success of sea-ranched salmon that have lived one year in nature is between that of wild and farmed Atlantic salmon coming directly from the net pens (Fleming et al. 1996, 1997). However, there is one example of high reproductive success of cultured fish. Dannewitz et al. (2004) found no significant difference in reproductive success between seventh-generation hatchery brown trout and wild-born brown trout in an experimental stream. Thus, hatchery fish may not always be an inferior competitor to wild fish on the spawning grounds.

The inferiority of hatchery fish is more pronounced in hatchery males than females, resulting in cross-breeding between hatchery females and wild males. In brown trout, hatchery-reared males seem to have lower reproductive success than wild males as found in an experimental stream, but no similar effect for females was reported (Dannewitz et al. 2004). Experimental evidence from Atlantic salmon suggests that the male fitness difference occurs because they arrive at the spawning grounds later than wild males, do not establish dominance hierarchies as effectively as wild males, court less, spawn with females in larger numbers, and partake in fewer spawnings, and they frequently fail to release sperm when the females release their eggs. On the spawning grounds, male hatchery Atlantic salmon are involved in more prolonged aggressive encounters, incur greater wounding, and have higher mortality than wild males originating from the same population (Fleming et al. 1996, 1997). The hatchery males ascend the spawning river later in the season, are less able to monopolize females, move about more in the river, and, after spawning, they leave the river earlier than wild fish originating from the same population. Hatchery salmon also return to sea without having spawned more often than wild salmon (Jonsson et al. 1990a).

Biomass and Production

Releases of salmon are meant to increase the productivity of habitats as found in the River Drammen by Hansen (1991), but hatchery production may decrease the productivity of the wild stock present. As a consequence of the spawning of hatchery salmon in the River Imsa, Fleming et al. (2000) found a 30% reduction in production of wild Atlantic salmon. Unwin and Glova (1997) found a 34% reduction in the production of wild Chinook salmon in a New Zealand river, probably due to density-dependent mortality caused by released hatchery fish. Furthermore, Nickelson (2003) reported decreased salmon production in Oregon coastal river basins and lakes where large numbers of cultured coho salmon smolts were released and recommended against such large releases in areas with high concentrations of wild fish. Chilcote (2003) maintained that removal rather than addition of hatchery fish may be the most effective strategy to improve productivity and resilience of steelhead. He found that populations consisting of equal numbers of cultured and wild fish produced 63% fewer recruits per spawner than one composed entirely of wild fish. In cases where fish releases result in a decrease rather than an increase in total population size, this may be due to a genetic change with the introduction of maladaptive traits or loss of genetic variation (Wang and Ryman 2001; Garcia de Leaniz et al. 2007) or an overexploitation of the food resources present with a resulting decrease in carrying capacity of the habitat. In some cases, there appear to be only minor effects of released cultured fish on the local wild populations, as reported by Hayes et al. (2004). When Goodman (2005) modeled the effects on natural spawning fitness in rivers where wild and cultured fish spawn together, he found potential, but not a certainty, for erosion of natural spawning fitness, a finding supported in the analysis of Naylor et al. (2005). Thus, there are variable results from an increased to decreased total production after releases of salmon, which are reasonable and depend on the environmental conditions where the fish are liberated. But most effects of releases of hatchery salmon seem negative.

Why Do Hatchery Salmon Often Perform Poorly in Nature?

The success of hatchery fish in nature is often low (e.g., Hjort and Schreck 1982; Swain et al. 1991; Fleming et al. 1994; Pelis and McCormick 2003; Kostow 2004; Von Cramon-Taubadel et al. 2005). Hatchery and wild conspecifics experience different environments before the release of the cultured fish. Hatchery salmon allocate more energy to protein growth and lipid deposition, and in association with this, several morphological changes occur (Fleming et al. 1994; Price 1999; Waples 1999). Hatchery tanks are space-restricted and simple; there is little seasonal change in environmental variables, high-quality food is readily available, and the fish are protected against predators and treated for some diseases. Furthermore, in hatcheries, salmon reproduce without having to compete for mates. On the other hand, hatchery fish are frequently disturbed by human treatment, and fish density is unnaturally high with the possibility of more social encounters, increased stress and aggression levels, and increased vulnerability to contageous diseases (Huntingford 2004).

Hatchery salmon deviate from wild salmon due to these differences in environments. The phenotype is both directly (plastic) and indirectly (genetic) influenced by the environment. Phenotypically plastic divergences are often shaped early in life. Von Cramon-Taubadel et al. (2005) found that the body form of Atlantic salmon parr grown from the eyed egg stage with a nonsibling group in a hatchery resembled the body shape of the nonsiblings more closely than the full siblings grown in their natal habitat. The morphological differences, however, are less pronounced after 1 year swimming freely in the sea (Fleming et al. 1994). Thus, some of the phenotypic differences caused by the rearing conditions disappear with time when the divergent groups are brought together in a common habitat.

Hatchery rearing also influences anatomic characters such as the development of the forebrain (telencephalon) of salmon and trout (Lema et al. 2005). It is found that cultured Pacific salmonids have smaller brains than wild conspecifics of similar size, but the reason is still unknown (Kihslinger and Nevitt 2006; Kihslinger et al. 2006). Furthermore, sensory organs such as the lateral system and eyes may be modified during hatchery rearing and influence the performance of hatchery fish in nature (Marchetti and Nevitt 2003; Anras and Lagardere 2004). Furthermore, it is found that brain gene expression profiles in Atlantic salmon is affected by rearing environment such as hatchery and river, as well as between reproductive tactics independent of rearing environment (Aubin-Horth et al. 2005).

Heart anatomy also differs between hatchery and wild salmonids. The normal shape of the salmonid ventricle is a triangular pyramid with the apex pointing caudoventrally. But Poppe et al. (2003) found that the hearts of hatchery-reared Atlantic salmon and rainbow trout were rounder than those in their wild counterparts and that the angle between the ventricular axis and the axis of the bulbus arteriosus was more acute in wild fish. Fish with abnormal heart morphology have higher mortality rate during stress-induced situations, and the cardiac output, heart rate and stroke volume, and active metabolic rate may be smaller (Dunmall and Schreer 2003; Claireaux et al. 2005).

Hatchery fish may be compromised in their ability to undergo smolting in terms of physiological changes needed to ionic regulation in marine waters. Lower gill Na+, K+ – ATPase activity, growth hormone, and plasma chloride levels of cultured than wild smolts was observed by Handeland et al. (2003), and survival on transfer to full-strength seawater at different temperatures indicates that wild Atlantic salmon smolts may tolerate the transfer better than cultured smolts. Handeland et al. (2003) concluded that the observed differences are genetic and associated with broodstock selection for rapid growth over several generations. On the other hand, such differences may well be phenotypic, linked to the seasonal development and size of the fish, as suggested by Ugedal et al. (1998), investigating seawater tolerance in cultured and wild smolts of brown trout. Hatchery Atlantic salmon smolts of the Irish Burrishoole stock had higher basal cortisol levels in April and May than wild smolts and did not exhibit the typical cortisol responses to capture stress. Similar differences were found in serum glucose levels, and cultured smolts had significantly higher concentrations of mucous cells in both skin and secondary gill lamellae, which may influence the subsequent marine survival (Poole et al. 2003).

Such phenotypic deviations results from (1) hatchery experiences, (2) developmental processes, and (3) physical damage incurred through hatchery rearing.

Hatchery Experiences

Cues sensed by fish influence behavioral traits (Brown et al. 2003) and differential juvenile experiences between hatchery and wild Atlantic salmon are likely to generate differences between them (Jonsson et al. 1990a; Huntingford 2004; Braithwaite and Salvanes 2005). For instance, early river experience influences the timing of the river entry for spawning (Jonsson et al. 1994; Skilbrei and Holm 1998), risk taking (Sundström et al. 2004), antipredator and feeding behavior (Reiriz et al. 1998; Brown and Laland 2001, 2002; Reinhardt 2001). Vilhunen et al.

(2005) reported that acquired predator recognition was socially transmitted from predator experienced to predator naïve conspecifics as found in experiments with Arctic char *Salvelinus alpinus*.

When released in nature, hatchery Atlantic salmon enter rivers to spawn (Jonsson et al. 1990a, 2003a; Clifford et al. 1998). However, their homing precision is less accurate than that of wild fish even when the two leave the river together as smolts (Jonsson et al. 2003a). Mean rates of straying of released hatchery versus wild Atlantic salmon of the River Imsa stock were estimated at 15% and 6%, respectively, and the more years the fish stayed away from the river, the larger was the straying rate. Both cultured and wild salmon strayed to many of the same rivers (ca. 80% of them drain into the fjord of the River Imsa within 60 km of the outlet).

Cues encountered by seaward migrating smolts influence the homing behavior of salmonids (Hansen et al. 1993; Dittman and Quinn 1996) and river ascent (Hansen and Jonsson 1994; Jonsson et al. 1994). Together, such observations indicate that differences in sensory stimulations between hatchery and wild salmon influence subsequent performance in nature. A more variable hatchery rearing environments might mitigate some of this difference between wild and hatchery salmon, as shown for hatchery-reared Atlantic cod *Gadus morhua* (Salvanes and Braithwaite 2006).

Developmental Processes

Developmental processes expressed by the phenotype are influenced by hatchery conditions. For instance, egg incubation temperature affects subsequent growth performance of the parr. In hatcheries, salmonid eggs are often incubated at elevated water temperature to induce early hatching and a prolonged first growing season. This gives the young fish a size advantage over similar-aged wild conspecifics when liberated in nature. This size advantage can influence the outcome of social encounters, with effects on other life history characters as previously explained.

Atlantic salmon parr are often faster growing in hatcheries than in nature owing to higher energy input and/or lower energy expenditure, with consequences for life history traits such as age and size at smolting (Økland et al. 1993), age at sexual maturity (Alm 1959; Vøllestad et al. 2004), and reproductive output (Jonsson et al. 1996). Fast-growing parr tend to smolt younger and smaller (Økland et al. 1993), but the size of hatchery smolts is variable and heavily dependent on smolt age (Jonsson et al. 2003b). Furthermore, high growth rate of female salmon in freshwater is associated with a relatively low growth increment at sea (Einum et al. 2002), and low growth increment at sea is associated with early age and small size at sexual maturity (Nicieza and Braña 1993; Jonsson and Jonsson 2004b). Gonadal mass and energy content increase with somatic mass in both sexes (Jonsson and Jonsson 2003), and as a reaction norm in Atlantic salmon, fast-growing parr tend to produce more and smaller eggs when they mature than if they grow more slowly (Jonsson et al. 1996; Fleming et al. 2003). In other species such as brown trout, coho salmon, and Chinook salmon, egg size and fecundity appear to be chiefly determined by the energy intake later in life and not flexibly dependent on the early, juvenile growth rate (Jonsson and Jonsson 1999; Quinn et al. 2004).

Lack of exercise in hatcheries may influence the hormone production of Atlantic salmon. Hatchery smolts challenged by a high current velocity are more active than the unchallenged smolts, probably because of elevated thyroxin level (Youngson and Webb 1992) with effects on the downstream smolt migration (Youngson et al. 1989; Iwata et al. 2003) and possibly the subsequent homing behavior (Dittman et al. 1996; Lema and Nevitt 2004). The hormone level can also be elevated if the hatchery smolts are retained for some time in so-called "imprinting ponds" with higher current velocity than experienced in hatcheries, before release (McCormick et al. 2003).

There is correlation between adiposy and maturation in salmonids (Rowe et al. 1991; Silverstein et al. 1999), and the lack of exercise in hatcheries influences lipid deposition, growth, swimming performance, and rate of fin healing, with possible effects on subsequent reproductive performance and success (Jørgensen and Jobling 1993). Male Chinook salmon reared in high-current velocity conditions started spawning 2.4 d earlier and defended their access to spawning females better than males reared in low-velocity tanks (Berejikian et al. 2003). Adult Atlantic salmon reared to smolting in high-velocity tanks enter freshwater for spawning more readily than those reared in a regular low-velocity environment (Skilbrei and Holm 1998). Patterson et al. (2004) reported effects of exercise on age at maturity, egg deposition rate, and egg survival in sockeye salmon *O. nerka*. Nonexercised females had delayed maturity, had lower egg deposition rates, and were more likely to die prior to ovulation and to exhibit poorer egg survival than exercised fish and wild spawners. Thus, lack of physical exercise by hatchery fish may diminish their success in nature relative to that of wild fish.

Physical Damages

Damage to the rayed fins of hatchery Atlantic salmon parr is primarily caused by aggressive encounters between fish with nipping of fins (Ellis et al. 2002), but may also result from abrasion on rough surfaces, nutritional deficiencies, and secondary bacterial infections (Höglund et al. 1997; Lellis and Barrows 1997; Latremouille 2003). The damaged or distorted jaws sometimes seen in hatchery salmon may also result from injuries in the tank environment, which hardly ever occur under natural conditions in rivers. While such damage incurred during culture can influence the performance of the fish and is therefore undesirable, it can be helpful when studying social interactions between groups of wild and hatchery fish (MacLean et al. 2000).

Genetic Diversity

Atlantic salmon segregate into distinct reproductive groups or local populations (Verspoor et al. 2007), and there is evidence of adaptive variation among the populations of Atlantic salmon (Hansen and Jonsson 1991b; Nislow et al. 2004; review in Garcia de Leaniz et al. 2007). In the hatcheries, however, salmon face new selection pressures, and the divergent phenotypic expression of hatchery relative to wild conspecifics can be influenced by natural selection in the hatchery conditions and artificial broodstock selection. Furthermore, hatchery populations may be influenced by genetic drift, inbreeding, and outbreeding depression.

The scale and extent of adaptive variations among salmon populations are poorly understood, but they depend probably on habitat heterogeneity, environmental stability, and the relative roles of selection and drift. As Garcia de Leaniz et al. (2007) maintained, maladaptation often results from phenotype–environment mismatch. To avoid this, one should act as if all populations are locally adapted. That means that one should minimize alterations to native populations and habitats to which populations may be adapted to and allow for population size to extend beyond the carrying capacity of the habitat to maintain genetic diversity and encourage competition and other sources of natural mortality required for natural or stabilizing selection.

Hatchery Selection

Population specific adaptations may be changed in hatcheries as artificial culture exposes fish to new selecting forces (Thorpe 2004). The genotypic change of cultured fish from their wild origin is a response to changed birth and/or death rates as a consequence of natural selection in the hatchery environment (Heath et al. 2003; Obedzinski and Letcher 2004). For instance, hatcheries appear to select for enhanced aggression in natural river environments, as found for Atlantic salmon (Einum and Fleming 1997), Chinook salmon (Wessel et al. 2006), coho salmon (Rhodes and Quinn 1998), masu salmon (Yamamoto and Reinhardt 2003), brown trout (Sundström et al. 2003), and rainbow trout (Riley et al. 2005). The higher aggressiveness may be linked to the high fish density in hatchery tanks. Glover et al. (2004) showed that the families of brown trout that survived best under conditions of abundant food were different from those that survived best on low rations.

Broodstock Selection

Farmed salmon selectively bred over several generations for production traits such as fast growth differ genetically from their wild origin when they are released in nature (Weber and Fausch 2003; McLean et al. 2005), with for example higher production rates of growth hormone (Fleming et al. 2002). The resulting fast growth is linked to enhanced appetite and greater risk taking (Fleming et al. 2002) and elevated standard metabolic rate (Metcalfe et al. 1995; Cutts et al. 2002; Lahti et al. 2002). Hybrid juveniles are often intermediate in character expression between hatchery and wild juveniles (McGinnity et al. 1997, 2003; Fleming et al. 2000). Thus, broodstock selection can cause correlated and unintended genetic changes. Hatchery salmon transported and released in new areas can deviate significantly from the local wild fish.

Selection for high growth rate, however, may reduce the aggressiveness of the fish. This was demonstrated in experiments with newly emerged brown trout fry (Hedenskog et al. 2002). Petersson and Järvi (2003) reported that wild juvenile brown trout were more aggressive than the offspring of sea-ranched brown trout and attacked novel objects sooner, a behavior that gives elevated dominance status (Sundström et al. 2004). Furthermore, Sundström et al. (2005) observed different responses of cultured and wild brown trout originating from the same stock, which may be caused by different selection regimes in the hatchery and nature (Huntingford and Adams 2005). In coho salmon, aggressiveness and growth rate are negatively correlated (Vøllestad and Quinn 2003), probably because the time spent on agonistic interactions reduces food consumption and/or increases the energy use. Thus, broodstock selection for production traits in hatcheries may counteract the selection for increased aggressiveness under hatchery conditions.

Selection response may also be obtained for a number of other traits such as sea survival and return rate (Jonasson et al. 1997), age at sexual maturity (Gjerde et al. 1994; Gjedrem 2000), disease and parasite resistance (Fjælestad et al. 1993; Gjøen et al. 1997; Kolstad et al. 2005), feed efficiency (Kolstad et al. 2004), and low percentage of sexually mature male parr (Wild et al. 1994). However, many such changes may be undesirable when restoring salmon populations.

Genetic Drift, Inbreeding, and Outbreeding

Genetic changes of the populations should be avoided when restoring salmonid populations (Cross 2000), as this may result in increased rate of hybridization with related species or with endemic populations of the same species and give elevated rates of genetic drift (Wang and Ryman 2001). Furthermore, within-population genetic diversity may be eroded by stocking large numbers of genetically similar individuals into small populations (Yokota et al. 2003). To decrease such hazards, Harada et al. (1998) advised that one should use wild-born parents of both sexes for broodstocks. On the other hand, Riley et al. (2004) found few significant ecological effects of small-scale releases of hatchery coho and Chinook salmon even when the wild conspecifics occurred at low densities, indicating that genetic effects of hatchery salmon on wild populations are variable.

Inbreeding with loss of heterozygosity may occur in hatcheries with negative effects on individual and population performance when released in nature because of reduced adaptability and accumulation of genes with detrimental effects (Wang et al. 2001; Primmer et al. 2003; Tiira et al. 2006). Garant et al. (2005) reported an increased reproductive success of females with a higher number of mates, resulting in more outbred offspring. Furthermore, Ayllon et al. (2004) suggested that poor planting success of Atlantic salmon introduced to streams of the Kerguelen Island, Antarctica was due to a too low genetic variability of the broodstock. Thus, enhanced genetic diversity of released hatchery fish may increase their reproductive success in nature.

As a management measure, new nonnative alleles can be introduced to populations with low genetic variability (Tallmon et al. 2004; Hedrick 2005; Edmands 2007). On the other hand, adding new alleles may be detrimental to populations if it breaks coadapted gene complexes important for fitness traits in the local environment (outbreeding depression). Little is known about the effects of outbreeding in salmon, but it may decrease fitness (Fleming et al. 2000; McGinnity et al. 2004) as in a variety of other species (Edmands 1999; McClelland and Naish 2007). Because of this, several authors advocate habitat restoration, if possible, rather than supportive breeding when supporting threatened or endangered populations (Ford 2002; Dannewitz et al. 2004; Almodovar et al. 2006).

A sufficient amount of genetic variation is required for the persistence of self-recruiting populations, and genetic variation is important for the survival and success of cultivated smolts in natural ecosystems. If the cultivated population has been through a bottleneck and the genetic variation is low, due to a low effective population size, the cultivated fish may suffer from inbreeding depression, reducing the fitness considerably. Hence, the release may be more harmful than good for the augmented population.

Conclusion

With all these differences between hatchery and wild fish, what is the main reason for the low success of hatchery salmon in nature? Most probably, a large part of the released hatchery salmon die because of predation soon after being released. The performance of hatchery fish in nature is highly influenced by their early experiences in the hatchery environment. Hatchery practices affect both genotype and phenotype of the fish and may produce an inadequate behavior versus predators. Thus, the time period the fish spend in the hatchery may be minimized to offer the fish maximum experience in natural environments. This implies that the size of the managed population will be regulated by natural mechanisms and factors in the systems. Alternatively, the complexity of the hatchery environment should be increased to produce fish exhibiting adequate avoidance behavior against predators.

Habitat Restorations and Enhancement

For Atlantic salmon, less is known about habitat restoration than on effects and successes of fish releases, and much knowledge gained is from experiments and management operations on other salmon species. However, the abundance and growth can be augmented through habitat manipulations improving feeding opportunities and water quality (Lacroix 1996; Hesthagen et al. 1999), increasing the spawning habitat by introducing gravel (Avery 1996; House 1996; Scruton et al. 1997), increasing the productive area by constructing side channels (Pethon et al. 1998), removing blockages and construct fishways (Saltveit 1989; Simenstad et al. 2005), and changing the flow regime (Armstrong et al. 2003). If the natural production of a river is to be restored, one should identify the constraints for salmon habitat use and relieve these constraints (Ebersole et al. 1997). One should keep in mind, however, that any river has a limited carrying capacity, although this may be increased to some degree by habitat improvements. To augment the population abundance, the easiest means may be to increase the exploitable area for the fish.

Fishways

Salmonid populations can be enhanced if the fish are allowed to colonizing new habitats upstream their original distribution area (Ritter 1997; Bryant et al. 1999). Such improvements may be accompanied by stocking programs to increase the colonization rate. The first step in colonizing new habitats is to provide free fish migration over natural and/or man-made barriers as waterfalls, dams, and turbines. Constructions of fishways and nature-like bypasses similar to natural streams facilitates the upstream migration for salmon.

Often, however, fishways can delay or prevent the upstream migration of Atlantic salmon. The fish may have problems in locating entrances and successfully ascending them. To help avoid this, Katopodis (2005) presents a toolkit for fish passages. It is essential that entrances are designed and located properly to enable and to stimulate fish ascent (Clay 1995; Larinier 1998). Spawners search for the highest flow (Williams 1998) and if the fish need to leap, a downstream deep pool is needed where fish can initiate jumps. If care is not taken, the fish may be attracted towards impassable routes from turbine outlets or dams rather than to the bypass (Andrew and Green 1960; Brayshaw 1967; Arnekleiv and Kraabøl 1996; Thorstad et al. 2003). For instance, upstream migrating salmon in the regulated River Tuloma, Kola Peninsula were rather reluctant to enter fish passes, occasionally even backing out after having entered the pass. The fish preferred to seek their way in strong current (i.e., the tailrace and spillway discharges below the Tuloma dam [Karppinen et al. 2002]). Upstream migrating Atlantic salmon in River Conon, northern Scotland were delayed and did not navigate through a series of four fish passes and an impoundment (Gowans et al. 2003). The proportion of the fish passing the individual obstructions ranged from 63% to 100%. No fish were lost when moving through the impoundment, whereas 63% of the approaching salmon passed each of the lifts. The fish were delayed for 1–41 d at a pool-and-overfall ladder and 1–52 d at a Borland fish lift. In the River Nidelva, south Norway, the salmon migrated quickly up to the tunnel outlet of the power station, but stayed on average 20 d (0–71 d) in the outlet area before continuing upstream (Thorstad et al. 2003). The size and design of the tunnel outlet, whether the outlet is submerged or not, and the slope of the tunnel appeared important for the salmon ascent.

Fishways can be size-selective. The Isohara fishway, close to the mouth of the regulated River Kemijoki, north Finland allowed one-sea-winter fish to pass (Laine et al. 1998). Larger, multi-sea-winter fish were observed close to the two alternative fish entrances without any attempt to enter. An inadequate fishway discharge together with poor attraction of the fish entrance was suspected to be the main reason for why they did not enter. After the entrance was replaced by a pool and a small waterfall, no more observations were made of salmon gathering close to the entrance, and the number and maximum size of the salmon increased in the fishway (Laine et al. 2002). The number of multi-sea-winter salmon passing through the fishway in the River Kemijoki was positively correlated with the mean tailwater level on the day of ascent and 1–3 d earlier. The tailwater level did not follow the river discharge but the seawater level, which was affected by the direction and velocity of the winds. Thus, the design of the entrance of the fishway is important, and a poor design is a migratory obstacle for the fish.

The colonization rate varies among species when new river stretches open for migratory fish. For example, the access of anadromous salmonids to the Margaret Creek water shed, southeast Alaska, previously blocked by a 7-m waterfall, was opened by a fish ladder constructed during 1989–1990. Pink salmon dominated numerically in the ladder during the subsequent 7-year study period (Bryant et al. 1999) and increased from 6,090 fish in 1991 to 39,499 fish in 1997. The number of sockeye and coho salmon passing the ladder ranged from 73 to 408 and 111–1,986, respectively. Few chum salmon *O. keta* and steelhead entered the ladder. Reasons for this may be that chum salmon does not ascend obstacles as easily as other anadromous species (Hale et al. 1985) and steelhead was less abundant in the watershed than other salmonids. Further examples of successful colonization of new areas by natural waterfalls by Atlantic salmon are described by Ritter (1997) from Torrent and Exploits rivers, west and east coast of insular Newfoundland and LaHave River, Nova Scotia.

Spawning Habitat Improvements

Gravelling can be a successful way of enhancing Atlantic salmon populations in rivers with reduced spawning opportunities (Merz and Setka 2004). For instance, gravel size, depth and compactness, and extent of suitable gravel available at the redd site affect density of redds in steelhead, in addition to water depth, velocity, and temperature (Orcutt et al. 1968). Spawning-bed enhancements have increased the survival and growth of Chinook salmon embryos in a regulated California stream (Merz et al. 2004). Salmon embryos planted in the improved spawning substratum exhibited higher rates of survival to the swim-up stage than embryos planted in the original spawning gravels. Furthermore, in the Mokelumne River, California Central Valley, 976 m^3 of clean river gravel (25–150 mm) was placed in berm and gravel bars along a 45-m enhancement site (Merz and Setka 2004). After gravel placement, the channel water velocities, intergravel permeability, and dissolved oxygen increased and the channel depth was reduced. Adult Chinook salmon began spawning at the previously unused site 2 month after gravel placement. However, in some cases, gravelling is not enough to create new salmonid spawning grounds (Zeh and Dönni 1994). In the River High-Rhine, Switzerland, washed gravel (grain size 16–50 mm) were introduced in an impounded section of the river to restore the spawning grounds for brown trout and Arctic grayling. Neither brown trout nor rainbow trout were observed spawning in the gravel beds. On the other hand, successful embryonic and larval development of grayling was observed, meaning that the new spawning area was suitable for this species.

Juvenile Habitat Improvements

Habitat preferences of salmonids vary with species and life stage and season (Heggenes et al. 1999). For instance, Atlantic salmon is distributed in faster-flowing habitats compared with brown trout, and often, but not always, they are associated with rivers with gravel bottom (Riley et al. 2006). The time as embryo in the bottom substratum and the transition from dependence on maternal yolk reserves to external feeding are critical periods. For instance, salmonid embryos are susceptible to fine-sediment infiltration during the incubation period (Julien and Bergerson 2006). In a field experiment, it was found that survival of pre-eyed, eyed, and hatched stages of Atlantic salmon were all negatively correlated with the percentage of fine sediment entering the incubation baskets. The pre-eyed and eyed stages were most strongly affected by silts and clays (<0.063 mm), although this size-class represented only a small fraction (0.03–0.41%) of the grain size inside. The hatched stage was most strongly correlated with the infiltration of medium sand (0.25–0.50 mm) material. On average, 66% of the implanted embryos survived to the pre-eyed stage of development compared to 63% for the eyed and 48% for the hatched stages of development.

At the commencement of external feeding, the fry are especially vulnerable to predators and adverse environmental conditions. The availability of slowly flowing habitats at the stream margins is crucial during the first month of independence (Armstrong and Nislow 2006). Atlantic salmon parr perform ontogenetic niche shifts, and later during summer, age-0 parr obtain high consumption rates over a wider range of current velocities (0.2–0.6 m/s) (Nislow et al. 1999), and the fish are often found in shallow riffle-chute habitats (Heggenes et al. 2002). Larger parr exploit even faster current velocities and greater water depths. During winter, the parr often hide in the gravel substratum or stay in deep and low-velocity habitats during daytime, but may seek more open feeding areas during night (Maki-Petays et al. 2004; Riley et al. 2006). High concentrations of fine sediment in the substratum degrades the habitat for steelhead parr (Suttle et al. 2004), and the same probably holds for juvenile Atlantic salmon in rivers, although there are differences in responses to substrate and cover among species (Sergeant and Beauchamp 2006). Thus, it appears important both to consider substrate conditions and current velocity and water level when restoring Atlantic salmon rivers (Armstrong et al. 2003; Hendry et al. 2003).

To manage salmon rivers well, it is important to protect existing high-quality habitats (Fullerton et al. 2006). For Pacific salmon, Roni et al. (2002) recommended that the restoration then should focus on connecting isolated high-quality fish habitats such as instream or off-channel habitats made inaccessible by culverts or other artificial obstructions. Removing small artificial barriers that hinder upstream migration of fish is a major task in riparian habitat restoration (O'Hanley and Tomberlin 2005). In cases where the juvenile habitat is highly degraded, such as in the case of hydropower developments, artificial fluvial habitat channels may be constructed to enhance the natural production of juvenile fish as successfully done in south-central Newfoundland (Enders et al. 2007). The introduction of boulder clusters in the river has been found to be another effective method of increasing the parr density of Atlantic salmon in rivers, as shown in Joe Farrell's Brook, Newfoundland (de Jong et al. 1997). Also, V-dams have proven to be effective in increasing juvenile density through the creation of a diverse pool habitat. Half-log covers increased the number of age-0 parr through an increased instream cover. The usefulness of the placement of boulder weirs appears however, to vary among species (Roni et al. 2006) and may be even more useful when restoring brown trout than Atlantic salmon rivers (Heggenes et al. 1999).

Atlantic salmon parr feed largely on larvae of aquatic insects (Lillehammer 1973), and the quality and quantity of the food are often viewed as important factors influencing the carrying capacity of salmon rivers (Jonsson et al. 1998). Presence of woody debris in streams is one factor influencing the abundance of insect larvae (Giannico and Hinch 2003; Milner and Gloyne-Phillips 2005); it provides greater surface areas for the growth of the prey species and shelter for the fish (Johnson et al. 2005). Furthermore, woody debris may give overhead cover that decreases predation risk and offer decreased contact between the fish. It also decreases the current velocity and thereby decreases the energetic costs of the fish in the streams (Crook and Robertson 1999). Presence of dead wood in streams is found to be profitable for the production in a number of salmonid species (Johnson et al. 2005; Fox and Bolton 2007). One way of providing woody debris in salmon rivers is to leave an effective riparian buffer zone along the banks where trees and other plants are allowed to grow undisturbed (Haberstock et al. 2000; Opperman and Merenlender 2004).

Liming of Acidified Rivers

Acidification of salmonid rivers represents a major threat to salmon production. Prominent physiological disturbances in fish exposed to acid water are failures in ionic regulation, acid–base regulation, circulation, and respiration, of which the first and last are held to be the primary causes of fish death in both acid and aluminum-rich water (McDonald 1983; Exley and Phillips 1988; Berntssen et al. 1997). Atlantic salmon is more sensitive to acid water than other naturally occurring salmonids in Scandinavia (Rosseland and Skogheim 1984), and the most sensitive stage is the smolt stage (Rosseland et al. 1986). Applications of crushed limestone in acidic rivers enhanced Atlantic salmon spawning habitat and improved the survival of juvenile salmonids (Staurnes et al. 1996). Liming of an acidic second-order stream, Fifteen Mile Brook, Canada, resulted in a twofold increase in the number of occasions where more than a few juvenile Atlantic salmon survived severe acidic episodes in the brook (Lacroix 1996). Densities of age-0 salmon were related to seasonal and interannual variability in pH, but they were always greater in the limed section than in the unlimed. Atlantic salmon consistently placed most of their redds (78%) in the limed section, and these were often on the limestone bar.

Water Level and Flow Regulation

Low river flow restricts the upstream migration of the fish. Low flow precludes salmon from entering small streams, and the effect is strongest for large fish early in the migration season (Jonsson et al. 1990b, 2007; Tetzlaff et al. 2005). A similar effect on migratory behavior is observed for brown trout, although the species is less sensitive than Atlantic salmon (Jonsson and Jonsson 2002). In the River Gudbrandsdalslågen, east Norway, Arnekleiv and Kraabøl (1996) found that ferox trout (large fish-eating brown trout) did not pass the outlet channel from the power station when the residual flow decreased below 20 m^3/s, and the upstream migration could be initiated by an artificial freshest of 60 m^3/s. Thus, increased water level at the time of migration may facilitate the upstream migration in rivers and streams suffering from low flow (Jonsson et al. 2007).

Changes in flow patterns due to impoundments or partial barriers may affect habitat and mortality of young fish living in the river. Sudden reduction in river flow may cause high mortality of juvenile Atlantic salmon and brown trout through stranding (Bradford 1997; Halleraker et al. 2003; Berland et al. 2004). The chance of stranding was higher when the water temperature was low (e.g., winter conditions < 4.5°C) compared with higher temperatures during late summer and early autumn. This is probably because of lower fish activity during the cold season and a substrate-seeking behavior. Stranding is not equal to mortality, as the fish can survive for several hours in the substrate after dewatering. A prolonged shut down procedure of the turbines in a regulated river decreased the stranding of salmon parr drastically under spring conditions. In an experiment with free-ranging parr and parr restricted to an area near the riverbank, Berland et al. (2004) found no stranding of free-ranging parr during rapid flow reductions during daytime. In the containment pen, the parr distributed themselves relatively evenly among the cells. They moved about more at changing than at stable flows, and most fish that were stranded were observed during rapid flow reduction at night. Thus, rapid reductions in water flow may cause increased mortality in salmon parr in shallow habitats if movements are restricted, and less abrupt water level fluctuations might be helpful to the fish.

Salmon Management and Research Tasks

Population or Habitat Restoration?

Restoration, rehabilitation, and enhancement of salmonid populations may draw on any of the techniques and methods mentioned earlier in this paper. The preferable approach will depend on the purpose of the activity, the status of the population, and the condition of the habitat. In a situation with weak or declining salmonid populations caused by increased mortality at sea due to climate change (Friedland et al. 2000; Jonsson and Jonsson 2004a), there may be a wish to (1) augment the bottlenecks of the juvenile production by restoring or rehabilitating the habitat, (2) increase the productive river area by building fishways to previously salmon-free habitats upstream, or (3) release fish to enhance the amount of seaward migration smolts.

The abundance of salmonid populations is variable with long-term trends upon which there are short-term fluctuations (Einum et al. 2003). From the 1980s onwards, the production of wild Atlantic salmon at sea has decreased gradually, viewed to be the beginning of a negative, long-term trend (Beaugrand and Reid 2003; Jonsson and Jonsson 2004a). Growth and survival rates have decreased at the same time that the populations exhibit younger sea-age at sexual maturity. The result is more relatively small one-sea-winter fish and fewer old, large adults (Jonsson and Jonsson 2004b; Boyland and Adams 2006). Since there is no sign of density dependent mortality in Atlantic salmon at sea (Jonsson et al. 1998; Niemelä et al. 2005), the population decline may be mitigated by an increased smolt output. Both habitat improvements and opening of new river and lake habitats for salmon are ways of expanding the carrying capacity of water courses. Furthermore, eggs may be planted if spawners are lacking, whereas parr releases can be successful if the spawning but not the juvenile rearing habitats are destroyed. Smolt release is a possible way of escaping a population regulatory bottleneck in freshwater, as is postsmolt release at sea. However, the latter may be avoided because of the risk of spreading the hatchery fish among rivers when they return to freshwater for spawning (Hansen and Jonsson 1991a).

Regulated rivers, characterized by rapid fluctuations in water flow and temperature, may offer poor juvenile rearing habitats favoring smolt releases before releases of younger fish. The marine mortality of hatchery Atlantic salmon released at the smolt stage is often very high owing to phenotypic changes caused by the juvenile rearing environment (Dannewitz et al. 2003), and inadequate behavior of hatchery fish towards predators (Brown and Laland 2001). In such cases, research efforts may be channeled to improving the sea-survival of the fish. Successful restoration and rehabilitation of salmon populations assume that the fish reproduce successfully. Reproductive success of released hatchery salmon is generally lower than that of wild conspecifics because of inadequate spawning behavior (Fleming et al. 1996, 1997, 2000). If a population is on the brink of extinction, the population may be saved by cryopreservation of spermatozoa in a gene bank (Gallant et al. 1993; Jodun et al. 2007) to be used for production and release of hatchery fish if and when the living conditions in the river are improved. There are also hatcheries serving as gene banks by keeping live fish (Bergan et al. 1991). This may be helpful in a critical situation, but with time, hatchery selection may gradually change such populations from their source populations. Hatchery preserved populations may also have a small genetic basis and be different from the original populations due to genetic drift, reducing their value as broodstock for supplementary releases. However, release of hatchery fish is the only known method to increase population sizes above the carrying capacity of the juvenile rearing habitat, when this is rehabilitated and enlarged to its maximum (e.g., by use of fishways).

Although stocking for population enhancement has been practiced by resource managers for more than 150 years, the general view now is that habitat restoration and rehabilitation are preferred over fish releases where these can be applied. Reasons are possible negative genetic effects on the local population and the risk of spreading contagious diseases from hatcheries. Hatchery salmon released in nature have in some cases led to loss of genetic variability due to a small effective population size of the stocked fish with introgression and adaptive divergences in wild populations (Crozier 1998; Utter 1998). Therefore, one has to balance the long-term risk of genetic change in natural fish populations against the immediate benefits of artificially increasing fish abundance (Tringali and Bert 1998). This is an often encountered trade-off for fisheries managers since genetics of weak populations are easily changed by massive releases because of the small size of the local gene pools. As long as there are wild spawners present and suitable opportunities for reproduction and juvenile rearing in rivers, it appears better to allow the fish to reproduce naturally than using spawners as broodstock for artificial rearing and release.

Adaptive Management

By using adaptive management practices (Miller et al. 1995), one can reduce uncertainty and improve the remedial actions in light of the results from a continued monitoring of the population in question (Figure 1). The establishment of restoration goals is often hindered by limited knowledge about the status of the population, the reason for long-term trends and short-term fluctuations, the role of specific components in the ecosystems exploited by the salmon, the vulnerability to loss of diversity, and the economic implications involved. Goal setting and the attainment of goals are also hindered because ecosystems are dynamic and populations and species evolve in response to selection pressures. Salmonid populations shift with changes in climate and human impacts, and they migrate among habitats. Consequently, even if we have a vision of a desirable future, it is difficult to foresee a precise pathway to its fulfillment. Management decisions are taken in the face of uncertainty, but by using the adaptive management technique, we gradually reduce uncertainty by a continued evaluation of the results used to improving the remedial actions. Furthermore, we have to view salmon as an integrated part of the ecosystem, meaning that they depend

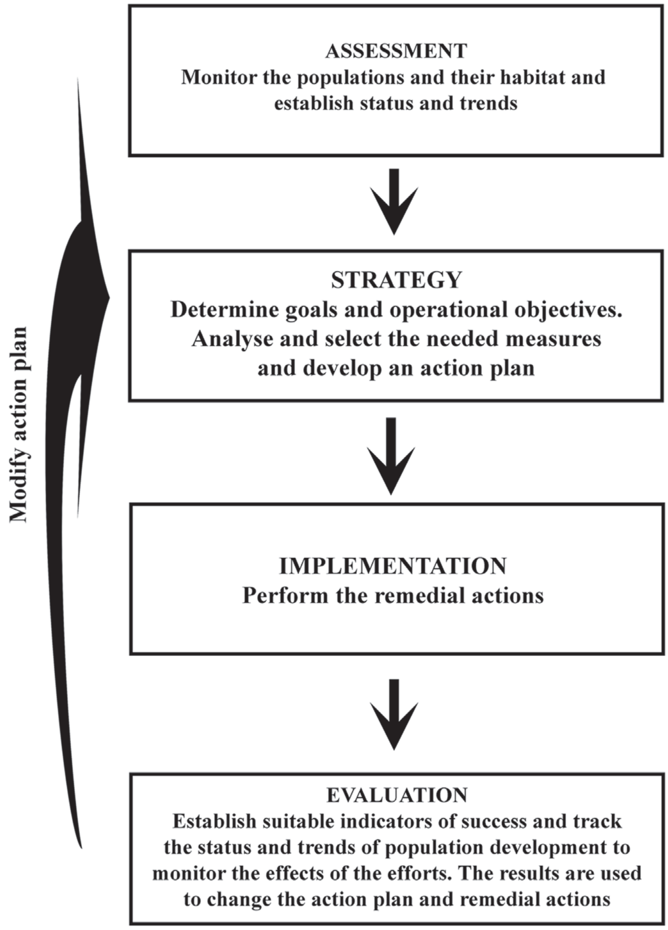

Figure 1.—Adaptive management of populations.

on the other components of their ecosystem. When restoring salmon populations and/or habitats, we therefore have to secure that the various needs for living in the habitat are fulfilled.

Density-dependent mechanisms constrain the parr production of freshwater habitats, as earlier explained. To manage Atlantic salmon population, one should monitor the habitats and densities of the age-groups of parr, establish status and trends, and compare the results with expectations based on experience from similar localities (Figure 1). Are parr densities significantly lower than found in good salmon rivers at similar latitudes? Are there too few young of the year or are older parr lacking? If the answer is yes to the first question, there may be a lack of spawners, the habitat may be unsuitable for spawning or early rearing, or the population is threatened by pollution (e.g., acidity, oxygen deficit, heavy metals) or a disease. These are all conditions that we may judge based on local knowledge, results of fishing efforts, observations on the spawning grounds, or experimental tests by use of, for instance, experiments such as planting eggs in incubation boxes buried in the spawning area or parr releases (see Population Restoration and Enhancement). If only older parr are lacking from the relevant habitats, they may have emigrated or an earlier year's recruitment has failed. At moderate and northern latitudes, there should at least be 1-year-old, if not older, parr, present. At southern localities, a large part of the smolt may be 1 year old, meaning that older parr can be naturally scarce.

Based on this assessment, one goals and operational objectives can be set. One may wish to restore inferior salmon habitats or open new areas of a river for salmon above a previously impassable water fall. Furthermore, the spawning stock may be small and needs to be increased. If this is difficult, an alternative is egg planting at suitable sites in the river. If there is a lack of parr, releases of parr or smolt may be required. One can determine required measures and develop and implement the remedial action plan to restore or enhance salmon populations.

By annual assessments of the populations, it is possible to evaluate the effects of the efforts and use the results to change the management strategy and actions to further improve the results in relation to any environmental or population change that might occur. Thus, the adaptive management program functions as a long-term experiment for optimal production of salmon rivers.

Research Tasks

An important research task is to breed a more wild-like phenotype than the regular hatchery salmon. To do that, we need new knowledge on how hatchery conditions change the fitness of cultured fish in nature. We need more information on the plasticity of the genotype–environment interactions and how hatchery conditions influence the fitness in the wild of liberated fish. For instance, how does the water current velocity influence hormonal changes and what are the phenotypic expressions of the affected individuals (McCormick et al. 2003)?

Elevated egg incubation temperature affects the subsequent metabolic and growth rates of the fish with possible effects on age and size at smolting and sexual maturity (Jonsson et al. 2005), but we lack a quantitative understanding of how important egg incubation temperature is for the subsequent maximum growth rate, optimal temperature for growth and growth efficiency (Jonsson et al. 2001), and life history characters associated with growth through norms of reaction (Jonsson and Jonsson 2004a). There is also a need for further studies on causes for the insufficient antipredator behavior of hatchery salmon and how this behavior can best be changed by modifying rearing facilities. Early habitat complexity influences later behavioral performance in Atlantic cod (Salvanes and Braithwaite 2006), and there is reason to believe that a similar relationship may hold for Atlantic salmon.

There is a need for new knowledge on how the habitat constrains salmon production. What are the mechanisms of density regulation, and how are the environmental conditions influencing population abundance (Einum and Nislow 2005)? Is winter or summer flow most limiting for the survival of young fish in rivers? How can flow in regulated river be modified to increase the smolt production? How is flow in fishways constraining adult fish size farther upstream? Furthermore, there is growing concern about ecosystem effects of hatchery salmon on communities and ecosystems (Pascual et al. 2002; Waknitz et al. 2003; Baxter et al. 2004). Salmon have the potential to reconstruct local food webs, and research is needed to evaluate this risk, especially when the species is spreads beyond its native range. Atlantic salmon is known as an ineffective colonizer (Naylor et al. 2005), but the current range represents colonization after the last glaciation period, meaning that there is a chance that releases in new areas may result in the establishment of self-sustaining populations.

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