

Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish

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When cultured Atlantic salmon are released into nature, they compete with wild fish for food, space, and breeding partners. As a result of morphological, physiological, ecological, and behavioural changes that occur in hatcheries, their competitive ability often differs from that of wild fish. These changes are partly phenotypic and partly genetic. Cultured juveniles' faster growth rate influences age and size at smolting and maturity, reproductive output, and longevity. Fast-growing parr tend to smolt younger, produce more but smaller eggs, attain maturity earlier, and die younger. Juvenile learning influences a number of behavioural traits, and differences in early experience appear to affect feeding and spawning success, migratory behaviour, and homing ability. Genetic change in hatcheries is chiefly the result of natural selection, with differential mortality among genotypes and broodstock selection based on production traits such as high adult body mass and fast growth rate. Experimental evidence has revealed that cultured parr's greater aggression often allows them to dominate wild parr, although smaller cultured parr can be subordinated if they co-occur in fast-flowing water and if wild smolts have established prior residence. During spawning, the fitness of wild salmon is superior to that of cultured conspecifics. Cultured males are inferior to wild males in intra-sexual competition, courting, and spawning; cultured females have greater egg retention, construct fewer nests, and are less efficient at covering their eggs in the substratum than their wild counterparts. In rivers, the early survival of cultured offspring is lower than that of their wild counterparts. The lifetime reproductive success of farmed fish has been estimated at 17% that of similar-sized wild salmon. As a result of ecological interaction and through density-dependent mechanisms, cultured fish may displace wild conspecifics to some extent, increase their mortality, and decrease their growth rate, adult size, reproductive output, biomass, and production.

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Introduction

Cultured Atlantic salmon (*Salmo salar*) are released both deliberately and unintentionally into nature. Intentional releases compensate for the decimation and sometimes for the elimination of wild populations owing to overexploitation, habitat alteration and destruction, and introduction of exotics such as the monogenean parasite *Gyrodactylus salaris*, which is lethal to young salmon in fresh water (Thorpe, 1998). Fish are also released in stocking and sea ranching programmes to augment harvestable resources (Wertheimer *et al.*, 2004b; Lorenzen, 2005). During the past 150 years, enhancement and supplementation have become essential parts of salmonid management (Wang and Ryman, 2001; McLean *et al.*,

2005). Cultured salmonids are released at all life stages, i.e. as eggs, alevins, fry, juveniles, and adults.

Unintentional releases occur when fish escape from hatcheries and fish farms. They exploit natural feeding areas in fresh water and at sea and may introgress natural stocks (Fleming *et al.*, 2000). Worldwide salmonid aquaculture production has grown rapidly during the past 30–40 years, from less than 200 000 t in 1970 to more than 1.5 million tonnes in 2000 (Tacon, 2003). With this increase, the escapement of cultured fish has also increased through regular low-level leakage and episodic events such as storms. It is estimated that approximately two million farmed salmon escape each year into the North Atlantic (Schiermeier, 2003). Between 1989 and 1996, 20–40%

of the salmon in the salmon fishery north of the Faroe Islands were of farmed origin (Hansen *et al.*, 1999; Jacobsen *et al.*, 2001). In Norwegian rivers, farmed salmon constitute an average of 11–35% of the spawning populations, but make up more than 80% of the spawning populations in some rivers (Fiske *et al.*, 2001; Naylor *et al.*, 2005).

With their short farming history, cultured salmonids are taking the first steps toward domestication and have been referred to as “exploited captives” (Balon, 2004). Cultured salmon survive and spawn in nature (Jonsson *et al.*, 1991a; Fleming *et al.*, 2000; N. Jonsson *et al.*, 2003), although they may have changed the form and behaviour of their wild origin to some extent (Gross, 1998).

Concerns have been expressed about the interaction between cultured and wild salmon, both in native habitats (Zimmerman and Nielsen, 2004) and when introduced elsewhere (Nash, 2003). Cultured fish can contribute to the loss or depletion of wild populations through predation and ecological competition for food, space, and breeding opportunities (Clifford *et al.*, 1998; Hard *et al.*, 2000; Fleming *et al.*, 2002), the spread of parasites and diseases (Johnsen and Jensen, 1991, 1994; Bakke and Harris, 1998; Krkosek *et al.*, 2005), and interbreeding with wild fish (Youngson and Verspoor, 1998; Fleming *et al.*, 2000; Lynch and O’Hely, 2001; Ford, 2002). Cultured and wild salmon interact at all stages of the life cycle and across the range of natural environments inhabited, and life history and fitness-related traits of the wild populations may be influenced (Jonsson *et al.*, 1991c; Thodesen *et al.*, 1999; McGinnity *et al.*, 2003). The ecological consequences of such interaction may be more pronounced when cultured salmon are an exotic species rather than an indigenous one (Gross, 1998), although Atlantic salmon exhibit poor colonizing ability outside their native range (Volpe *et al.*, 2000, 2001).

The influence of cultured fish on conspecific populations in the wild may be positive, neutral, or negative (Egidius *et al.*, 1991; Hindar *et al.*, 1991), but many cases reveal the harmful effects of cultured fish (Ricker, 1972; Hindar and Jonsson, 1995; Goodman, 2005). Interaction is likely to have a negative effect on the variability of wild populations (Youngson and Verspoor, 1998; Wang and Ryman, 2001), and authors have long cautioned against the escape of farmed salmon, both inside and outside the salmon’s native range (Reisenbichler and McIntyre, 1977; Hindar *et al.*, 1991; Soto *et al.*, 2001). Gross (1998) estimated a 5% probability that escaped and invading cultured Atlantic salmon would have a negative impact on wild populations. Naylor *et al.* (2005) demonstrated that the risk of damage to wild salmon populations and ecosystems is great when farmed salmon escape in their native range, when their numbers are large relative to the abundance of wild fish, and when exotic pathogens are introduced and spread by the farmed fish. Less is known about the possible effects outside the species’ native range (Waknitz *et al.*, 2003).

In this review, we summarize changes in morphology, physiology, and life history that occur in hatcheries and

consider characteristics that may affect the outcome of ecological interaction with wild conspecifics during feeding and spawning. Thereafter, we assess the causes of altered traits and summarize knowledge of the competition between cultured and wild salmon in nature, emphasizing the ecological significance of interaction. Finally, we recommend topics for future research that we feel would facilitate understanding of the issues reviewed and inform management of their importance. Atlantic salmon is the focal species, but we also address findings about other closely related salmonids, when appropriate. Because there have been several reviews of the interaction between cultured and wild salmonids in nature (e.g. Jonsson, 1997; Youngson and Verspoor, 1998; Weber and Fausch, 2003), we focus on the most recent literature but include some information from previous sources to make our review more comprehensive. However, we review only briefly the genetic effects of interaction and do not consider disease and parasite interaction, because these issues are reviewed by others in this volume.

Changing characteristics in cultured salmon

Morphology, physiology, and anatomy

Artificial culture exposes fish to new developmental forces that may shape the phenotypes, and thereby influence subsequent performance in nature (Table 1). The protected environment permits fish to allocate more energy to protein growth and lipid deposition, and several morphological changes occur in association with this (Thorpe, 2004). For example, cultured Atlantic salmon parr have smaller heads and rayed fins and narrower caudal peduncles than wild parr (Fleming *et al.*, 1994). Similarly, cultured juvenile coho salmon (*Oncorhynchus kisutch*) have smaller heads and relatively deeper bodies than wild conspecifics (Taylor, 1986; Swain *et al.*, 1991). The changed morphology probably influences the survival and growth of cultured fish in nature (Sheehan *et al.*, 2005; von Cramon-Taubadel *et al.*, 2005).

A similar morphological divergence exists between wild and cultured Atlantic salmon smolts from the Irish Burrishoole and Corrib stocks. In Burrishoole stocks, wild smolts are thinner and smaller. Furthermore, they have higher basal cortisol levels in April and May and do not exhibit the typical cortisol responses to capture stress exhibited by cultured smolts. Similar differences appear in serum glucose levels. Cultured smolts have significantly higher concentrations of mucous cells in both skin and secondary gill lamellae, which may influence subsequent marine survival (Poole *et al.*, 2003). These physiological changes, together with lower gill Na⁺/K⁺-ATPase activity, lower growth hormone and plasma chloride levels found in cultured smolts (as compared with wild smolts), and differences in survival on transfer to full-strength seawater at different temperatures (Handeland *et al.*, 2003), indicate that wild

Table 1. Morphological, physiological, anatomical, and life history characteristics of salmonids that change from the wild phenotype during hatchery rearing; h = hatchery fish, w = wild fish.

| Life stage | Changed characteristic | Difference | Sources |
|-------------------------------------|---|------------|--|
| Morphology | | | |
| Parr | Head | h < w | Taylor, 1986; Swain <i>et al.</i> , 1991; Fleming <i>et al.</i> , 1994; von Cramon-Taubadel <i>et al.</i> , 2005 |
| | Rayed fin | h < w | Fleming <i>et al.</i> , 1994; Fleming and Einum, 1997; Fiske <i>et al.</i> , 2005 |
| | Caudal peduncle | h < w | Fleming <i>et al.</i> , 1994 |
| | Body depth | h > w | Taylor, 1986; Swain <i>et al.</i> , 1991; Fleming and Einum, 1997; von Cramon-Taubadel <i>et al.</i> , 2005 |
| Smolts | Body size | h > w | Poole <i>et al.</i> , 2003 |
| | Condition factor | h > w | Sundell <i>et al.</i> , 1998; Poole <i>et al.</i> , 2003; von Cramon-Taubadel <i>et al.</i> , 2005 |
| Adults | Head | h > w | Fleming <i>et al.</i> , 1994 |
| | Rayed fin | h < w | Fleming <i>et al.</i> , 1994 |
| | Adipose fin | h > w | Fleming <i>et al.</i> , 1994 |
| | Caudal peduncle | h > w | von Cramon-Taubadel <i>et al.</i> , 2005 |
| | Body depth | h > w | Fleming <i>et al.</i> , 1994; von Cramon-Taubadel <i>et al.</i> , 2005 |
| | Distorted jaw | h > w | Fleming <i>et al.</i> , 1994 |
| | Damaged kype | h > w | Fleming <i>et al.</i> , 1994 |
| Physiology and anatomy | | | |
| Smolts | Cortisol level | h < w | Poole <i>et al.</i> , 2003 |
| | Glucose level | h < w | Poole <i>et al.</i> , 2003 |
| | Mucous cells | h > w | Poole <i>et al.</i> , 2003 |
| | Na ⁺ /K ⁺ -ATPase | h < w | Sundell <i>et al.</i> , 1998; Handeland <i>et al.</i> , 2003 |
| Adults | Heart abnormality | h > w | Poppe <i>et al.</i> , 2003; Seierstad <i>et al.</i> , 2005. |
| | Brain size | h < w | Marchetti and Nevitt, 2003; Lema <i>et al.</i> , 2005 |
| | Metabolic rate | h > w | Dunmall and Schreer, 2003; Claireaux <i>et al.</i> , 2005 |
| Life history characteristics | | | |
| Parr | Growth rate | h > w | B. Jonsson <i>et al.</i> , 1991a; Jonsson and Fleming, 1993; Kostow, 2004 |
| | Survival | h > w | B. Jonsson <i>et al.</i> , 1991a; Jonsson and Fleming, 1993; Kostow, 2004 |
| Smolts | Age | h < w | Oppedal <i>et al.</i> , 1999; N. Jonsson <i>et al.</i> , 2003 |
| Post-smolts | Survival | h < w | Piggins and Mills, 1985; B. Jonsson <i>et al.</i> , 1991a; N. Jonsson <i>et al.</i> , 2003; Saloniemi <i>et al.</i> , 2004 |
| Adults | Age at maturity | h < w | N. Jonsson <i>et al.</i> , 2003; Kostow, 2004 |
| | Longevity | h < w | Kostow, 2004 |

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 brood-stock selection for rapid growth over several generations, although such differences may well be phenotypic, i.e. linked to seasonal development and fish size, as suggested by Ugedal *et al.* (1998) after investigating seawater tolerance in cultured and wild brown trout (*Salmo trutta*) smolts.

Cultured post-smolts often exhibit minor scale loss (<5% of the body) and fin damage especially on the dorsal fin, caused mainly by intraspecific aggression during

juvenile rearing, in contrast to their wild counterparts (MacLean *et al.*, 2000; Fiske *et al.*, 2005; Lacroix and Knox, 2005). At maturity, farmed Atlantic salmon display morphology that differs greatly from that of wild fish. Farmed adults have longer heads, smaller rayed fins, larger adipose fins, shorter horizontal trusses in the trunk region, and more distorted jaws (Fleming *et al.*, 1994). Farmed males display more damage to their kypes and jaw distortion than wild males, which are almost free of such deformities. Sea-ranched and farmed Atlantic salmon also differ morphologically; sea-ranched adults have a more streamlined body,

shorter head, larger rayed fins, and a smaller adipose fin than farmed adults retained in sea pens. Sea-ranched males also display less damage to their kypes and less jaw distortion than farmed salmon. Such morphological differences may be important to subsequent reproductive success (Fleming *et al.*, 1996, 1997).

Hatchery rearing appears to influence forebrain development (telencephalon) of salmon and trout (Lema *et al.*, 2005). For example, cultured rainbow trout (*Oncorhynchus mykiss*) and coho salmon have smaller brains than wild conspecifics of similar size. It is not known whether the reduced cell proliferation of the telencephalon of juvenile fish is associated with swimming activity, sensory input, or social structure in the hatchery tanks, but Marchetti and Nevitt (2003) found that it may influence cultured salmonids' subsequent behavioural performance in nature.

The heart anatomy of cultured salmonids can also differ from that of wild salmonids. The normal shape of the salmonid ventricle is a triangular pyramid with the apex pointing caudo-ventrally. Poppe *et al.* (2003) found that the hearts of farmed Atlantic salmon and rainbow trout were rounder than those of their wild counterparts and that the angle between the ventricular axis and the axis of the *bulbus arteriosus* was less acute in farmed fish than in their wild counterparts. Fish with abnormal heart morphology have a greater mortality rate during stress-inducing situations such as grading, transportation, and bath treatments. Cardiac output, heart rate, and stroke volume do not necessarily differ in cultured and wild salmon (Dunmall and Schreer, 2003), but fish with decreased maximum cardiac performance have lower active metabolic rates and are poorer swimmers (Claireaux *et al.*, 2005). Therefore, lower survival, less reproductive success, and fewer competitive abilities can be expected in cultured salmon in nature.

Life history characteristics

As with morphology and physiology, hatchery rearing may influence the development of life history traits. Usually, wild salmonid parr and smolts are shorter and lighter than cultured fish of similar age (Jonsson *et al.*, 1991a; Kostow, 2004). Furthermore, cultured smolts are often more uniform in age distribution than wild smolts. Cultured Atlantic salmon can smolt at 1 year of age and after photoperiod manipulation during their first autumn, although wild conspecifics at the same latitude usually smolt at 2 or 3 years of age (Oppedal *et al.*, 1999; N. Jonsson *et al.*, 2003). The younger and less variable age at which cultured salmon smolt corresponds to the younger and less variable age at which they reach first maturity, with reduced longevity as a consequence. The longevity of cultured steelhead trout (*O. mykiss*) may be reduced by 1–3 years (Kostow, 2004). The changed growth rate and adult size influence reproductive output such as egg size, fecundity, and total gonadal mass (Thorpe *et al.*, 1984; Jonsson *et al.*, 1996).

Increased within-clutch variation in egg size is also possible (Einum and Fleming, 2004).

Differences in survival between wild and cultured salmonids are well documented. Jonsson and Fleming (1993) reported that the mean survival of wild Atlantic salmon from egg to smolts is 1.7% (range 0.14–6.5%). The freshwater survival in corresponding cultured fish may be approximately 20 times higher. First-year survival of more than 60% has been observed in cultured steelhead trout, compared with <2% and <1% for naturally produced winter steelheads and summer steelheads, respectively (Kostow, 2004). Therefore, cultured salmonids produce significantly more smolts per parent than wild fish, creating a selective difference between types.

Poor survival during free ranging at sea reverses the freshwater survival superiority of cultured salmon over wild salmon. Jonsson and Fleming (1993) estimated the mean sea survival of wild Atlantic salmon at 6.9% (2–20.8%), and it is higher for one-sea-winter salmon than for older salmon (Jonsson *et al.*, 1991c, 1997). In the Burrishoole stock, the smolt-to-adult survival of one-sea-winter wild salmon averaged 8% (2.9–12.6%), but only 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 (N. Jonsson *et al.*, 2003). In the Baltic Sea, the smolt-to-adult survival was 4.5 times higher in wild salmon than in cultured salmon (Saloniemi *et al.*, 2004). The difference in sea survival was more pronounced in low- than in high-survival years. In good years, the cultured smolts' larger size compensated for inferior performance compared with wild smolts, but in poor survival years, wild smolts always survived better. The estimated mean smolt-to-adult survival of naturally produced steelheads was 5–6%, whereas that of cultured stocks was approximately 1%, and total egg-to-adult survival was 0.05% for wild fish and 0.56% for cultured fish (Kostow, 2004). The sea survival of wild salmon, which is 3–5 times higher than that of cultured salmon released into rivers as smolts, may be linked to more relaxed selection pressure in hatcheries than in nature, as well as the phenotypic divergences of cultured fish from wild fish previously mentioned (Jonsson and Fleming, 1993; Reisenbichler and Rubin, 1999; Ford, 2002).

Why do cultured fish diverge from their wild origin?

The environments experienced by cultured and wild salmon are rather different (Price, 1999; Waples, 1999). On one hand, hatchery tanks are space-restricted and simple, i.e. provide limited sensory input, with no migratory possibility. They offer little seasonal change because high-quality food is readily available, and fish are protected against

predators and treated for some diseases. Furthermore, cultured salmon in hatcheries reproduce without having to compete for mates. On the other hand, cultured fish are frequently disturbed by human treatment, and fish density is unnaturally elevated with a higher number of social encounters, raised stress and aggression levels, and increased vulnerability to certain diseases (Huntingford, 2004).

The divergence of cultured fish from their wild origin is both phenotypic (environmental) and genetic (e.g. Hjort and Schreck, 1982; Fleming and Gross, 1989; Swain *et al.*, 1991; Fleming *et al.*, 1994; Pelis and McCormick, 2003; Kostow, 2004; von Cramon-Taubadel *et al.*, 2005). Because juvenile mortality in nature is very high but most fish may survive in a hatchery, the distribution of wild juvenile phenotypes should be a subset of cultured juvenile phenotypes. However, for some morphological characteristics, a large proportion of wild juveniles have phenotypes that are more extreme than those of cultured juveniles when the two originate in the same stock, although most of the cultured offspring have survived (Fleming *et al.*, 1994). In such cases, a genetic explanation does not seem likely, and the difference observed may largely reflect phenotypically plastic responses to different environments, including physical damage in culture. An experimental study, in which the eggs of wild and seventh-generation cultured brown trout were planted in a river, revealed significant differences in growth or survival when family and male–female effects were accounted for. This indicates that differences in performance between cultured and wild fish, at least in some cases, are phenotypic and caused by the juvenile rearing environment (Dannewitz *et al.*, 2003). It should be emphasized, however, that the phenotypic plasticity, i.e. the ability of a genotype to produce distinct phenotypes when exposed to different environments, is also a property of the genotype, both response pattern and degree of variability being shaped by natural selection (Pigliucci, 2005).

Phenotypic divergence

Phenotypic divergences can be shaped by environmental conditions early in life. Through discriminant function analysis, von Cramon-Taubadel *et al.* (2005) found a strong environmental effect on the body form of salmonid parr. Atlantic salmon parr grown from the eyed-egg stage with a non-sibling group in a hatchery environment came to resemble the body shape of the cultured non-sibling fish more closely than that of full siblings grown in their natal habitat. Moreover, the shape of wild smolts differed from that of cultured offspring. Although this difference was less pronounced, it was still significant when the fish were captured after free-swimming at sea for 1 year. Therefore, rearing conditions have a significant impact on fish body shape; some differences are phenotypic and disappear with time when the divergent groups are brought together in a common habitat (Fleming *et al.*, 1994).

The phenotypic deviations, summarized in Table 2, are short-term individual responses developed as a result of: (i) sensory stimulations, or lack of them, in the hatchery environment, (ii) biochemical and physiological processes that may adapt the organism to the environment, (iii) damage incurred through rearing, or (iv) developmental responses linking the environmental variable with the phenotypic expression (reaction norms *sensu* Stearns, 1992).

Sensory stimulation

Cues sensed by fish influence a number of behavioural traits (Brown *et al.*, 2003b), and differential juvenile experiences are likely to generate differences between cultured and wild fish (Huntingford, 2004). For example, early river experience influences timing of the river entry for spawning (Jonsson *et al.*, 1990; Jonsson, 1994; Skilbrei and Holm, 1998), risk taking (Sundström *et al.*, 2004), and feeding behaviour (Reiriz *et al.*, 1998). The tendency of farmed salmon to feed closer to the surface than wild fish is at least partly learned. In experiments with masu salmon (*Oncorhynchus masou*), Reinhardt (2001) reported that, over time, wild fish fed closer to the surface, although not as high in the water column as their cultured conspecifics.

On spawning grounds, sea-ranched male Atlantic salmon, probably resulting from their experience of feeding competition in hatchery tanks, took part in more prolonged aggressive encounters, incurred greater wounding, and sustained greater mortality than wild males originating in the same population, even though the two showed similar levels of aggression (Fleming *et al.*, 1997). Sea-ranched salmon ascended the spawning river later in the season, were less able to monopolize spawnings, moved about more in the river, and left the river after spawning earlier than wild fish originating in the same population. Sea-ranched salmon returned to sea without spawning more often than wild salmon (Jonsson *et al.*, 1990). In addition, in salmon (*Salmo* and *Oncorhynchus*), cues encountered by seaward-migrating smolts influence their homing behaviour (Hansen *et al.*, 1993; Dittman and Quinn, 1996) and river ascent (Hansen and Jonsson, 1994; Jonsson *et al.*, 1994). Taken together, such observations indicate that differences in sensory stimulation between cultured and wild salmon influence subsequent performance in nature, such as homing precision, feeding, migration, and spawning behaviour (Jonsson *et al.*, 2003a).

Biochemical and physiological processes

Developmental processes expressed by the phenotype are influenced by hatchery conditions. For example, egg incubation temperature affects subsequent parr growth performance. In hatcheries, salmonid eggs are often incubated at elevated water temperature to induce early hatching and prolong the first growing season. This gives young cultured fish a size advantage over wild conspecifics of similar age if released into nature. This size advantage can

Table 2. Sensory stimulations, biochemical and physiological processes, physical damage, and developmental responses that differ in salmonids in hatcheries and in nature, and that influence fish performance.

| Life stage | Environmental difference | Performance trait changed | Sources |
|---|---------------------------|--|---|
| Sensory stimulations | | | |
| Adults | Tank vs. river experience | Time of ascent | Fleming <i>et al.</i> , 1997; Skilbrei and Holm, 1998; B. Jonsson <i>et al.</i> , 1990; N. Jonsson <i>et al.</i> , 1994 |
| | | Risk taking | Berejikian, 1995; Fleming <i>et al.</i> , 2002; Sundström <i>et al.</i> , 2004 |
| | | Feeding behaviour | Reiriz <i>et al.</i> , 1998; Reinhardt, 2001; Sundström and Johnsson, 2001; Brown <i>et al.</i> , 2003a, c |
| | | Aggressive behaviour | Einum and Fleming, 1997; Rhodes and Quinn, 1998; Sundström <i>et al.</i> , 2003; Yamamoto and Reinhardt, 2003; Riley <i>et al.</i> , 2005 |
| | | River movement | B. Jonsson <i>et al.</i> , 1990; Økland <i>et al.</i> , 1995 |
| | | River stay | B. Jonsson <i>et al.</i> , 1990 |
| | | Straying to foreign rivers | Hansen <i>et al.</i> , 1993; B. Jonsson <i>et al.</i> , 2003 |
| | | Predator recognition | Brown and Smith, 1998; Mirza and Chivers, 2000; Berejikian <i>et al.</i> , 2003b; Vilhunen <i>et al.</i> , 2005 |
| | | Refuge use | Griffiths and Armstrong, 2002; Orpwood <i>et al.</i> , 2004 |
| Biochemical and physiological processes | | | |
| Egg | Incubation temperature | Growth rate | Rungruangsak-Torrissen <i>et al.</i> , 1998, 1999; N. Jonsson <i>et al.</i> , 2005 |
| | | Protein synthesis | Rungruangsak-Torrissen <i>et al.</i> , 1998, 1999 |
| | | Maintenance ration | Rungruangsak-Torrissen <i>et al.</i> , 1998, 1999 |
| Parr | Current velocity | Hormone profile | Youngson and Webb, 1992; McCormick <i>et al.</i> , 2003 |
| | | Adiposity | Rowe <i>et al.</i> , 1991; Silverstein <i>et al.</i> , 1999 |
| | | Maturity age | Patterson <i>et al.</i> , 2004 |
| | | Swimming performance | McDonald <i>et al.</i> , 1998; Claireaux <i>et al.</i> , 2005 |
| | | Fin healing | Jørgensen and Jobling, 1993 |
| Adults | | Spawning time | Berejikian <i>et al.</i> , 2003a |
| | | Courting and spawning behaviour | Fleming <i>et al.</i> , 1996, 1997 |
| | | River ascent | Skilbrei and Holm, 1998; N. Jonsson <i>et al.</i> , 1994 |
| Physical damage in hatchery | | | |
| Parr | Aggressive encounters | Fin damage | Höglund <i>et al.</i> , 1997; Lellis and Barrows, 1997; Ellis <i>et al.</i> , 2002; Latremouille, 2003 |
| | | Scale loss | MacLean <i>et al.</i> , 2000; Lacroix and Knox, 2005 |
| Developmental responses | | | |
| Parr | Higher growth rate | Smolt age | Økland <i>et al.</i> , 1993; Yamamoto and Morita, 2002; Duston <i>et al.</i> , 2005 |
| Adult | | Maturity age | Nicieza and Braña, 1993; B. Jonsson and N. Jonsson, 2004 |
| | | Longevity | B. Jonsson <i>et al.</i> , 1991b |
| | | Fecundity, egg mass, and reproductive output | N. Jonsson <i>et al.</i> , 1996; Tamate and Maekawa, 2000; Fleming <i>et al.</i> , 2003; Quinn <i>et al.</i> , 2004 |

influence the outcome of social encounters, with possible effects on other life history characteristics such as growth rate, age, and size at smolting and sexual maturity (Jonsson and L'Abée-Lund, 1993; Jonsson *et al.*, 2005). Furthermore, Rungruangsak-Torrissen *et al.* (1998) found different trypsin isozymes in Atlantic salmon hatching at 6 °C and at 10 °C. The various trypsin isozyme variants influence the

maintenance ration and capacity for protein synthesis in white muscle differently, affecting growth, size, and other life history traits (Rungruangsak-Torrissen *et al.*, 1999).

Hormone production, with effects on subsequent performance, can be influenced by fish activity. Atlantic salmon smolts challenged by high current velocity are more active than unchallenged smolts, probably because of an altered

hormone profile, e.g. elevated thyroxine level (Youngson and Webb, 1992), with effects on downstream smolt migration (Youngson *et al.*, 1989; Iwata *et al.*, 2003) and possibly on subsequent homing behaviour (Dittman *et al.*, 1996; Lema and Nevitt, 2004). However, the hormone profiles may return to normal if smolts are retained for some time before release in so-called "imprinting ponds" with greater current velocity than is experienced in hatcheries (McCormick *et al.*, 2003).

A correlation exists between adiposity and maturation in salmonids (Rowe *et al.*, 1991; Silverstein *et al.*, 1999), and exercise influences lipid deposition, growth, swimming performance, and rate of fin healing, with possible effects on subsequent reproductive performance and success in nature (Jørgensen and Jobling, 1993). Chinook salmon (*Oncorhynchus tshawytscha*) reared in fast current conditions started spawning 2.4 days earlier and defended their access to spawning females better than males reared in low velocity tanks (Berejikian *et al.*, 2003a). Therefore, flow rate may influence hormonal changes during maturation and behavioural performance of salmon. Moreover, Atlantic salmon reared in high velocity tanks appear to enter fresh water 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 (*Oncorhynchus nerka*). Non-exercised females experienced delayed maturity, lower egg deposition rates, and were more likely to die before egg ovulation and to exhibit poorer egg survival than exercised fish and wild spawners. Lack of physical exercise by cultured fish may diminish their success in nature relative to that of wild fish.

Damage incurred through hatchery rearing

Damage to the rayed fins of cultured fish is caused primarily by aggressive encounters between fish involving the 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). Although such damage incurred during culture can influence fish performance, and is therefore undesirable, it can be helpful when studying social interaction in large groups of fish (MacLean *et al.*, 2000). The damaged kypes and distorted jaws of cultured salmon may also result from injuries in the tank environment, which occur infrequently under natural river conditions.

Developmental responses

Salmon parr usually grow faster in hatcheries than in nature owing to a 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), and reproductive output (Jonsson *et al.*, 1996). Fast-growing parr tend to smolt younger and smaller

(Økland *et al.*, 1993), but the size of cultured smolts is variable and heavily dependent on smolt age (N. Jonsson *et al.*, 2003). Furthermore, the high growth rate of female salmon in fresh water is associated with a relatively low growth increment at sea (Einum *et al.*, 2002), which in turn appears to be linked to early age and small size at sexual maturity (Niecieza and Braña, 1993; Jonsson and Jonsson, 2004). 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 grew more slowly (Jonsson *et al.*, 1996; Fleming *et al.*, 2003). In other species such as brown trout, coho, and chinook salmon, egg size and fecundity appear to be determined chiefly by energy intake later in life and are not flexibly dependent on the early juvenile growth rate (Jonsson and Jonsson, 1999; Quinn *et al.*, 2004).

Genetic divergence

The genotypic change of cultured fish from their wild origin is a long-term response caused largely by changed birth and/or death rates, through alterations in gene and genotype frequencies as a consequence of natural selection in the hatchery environment (Heath *et al.*, 2003) and artificial broodstock selection for certain production traits (Gjedrem, 2000; McLean *et al.*, 2005). For example, selection in hatcheries appears to enhance aggression, as indicated by findings for Atlantic salmon (Einum and Fleming, 1997), 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). Greater aggression may be linked to high fish density in hatchery tanks, and Glover *et al.* (2004) showed that the families of brown trout that survive best under conditions in which food was abundant are different from those that survive best on low rations. Moreover, farmed salmon, selectively bred over several generations for production traits such as fast growth, differ genetically from their wild origin (Gjedrem, 2000; Weber and Fausch, 2003), with greater production rates of growth hormone, for example (Fleming *et al.*, 2002). Fast growth is linked to enhanced appetite and greater risk taking (Fleming *et al.*, 2002), and elevated standard metabolic rate (Metcalf *et al.*, 1995; Cutts *et al.*, 2002; Lahti *et al.*, 2002). Hybrid juveniles are often intermediate in their expression of characteristics between farmed and wild juveniles (McGinnity *et al.*, 1997, 2003; Fleming *et al.*, 2000). Therefore, broodstock selection can create differences in addition to those that were the target of selection. Because cultured salmon may be moved and released into new areas, they can differ significantly from local wild fish.

Hatchery selection for fast growth, on the other hand, may also reduce aggression. This has been demonstrated in experiments with newly emerged brown trout fry (Hedenskog *et al.*, 2002). Petersson and Järvi (2003)

reported that wild juvenile brown trout are more aggressive than the offspring of sea-ranched brown trout and attacked novel objects sooner, a behaviour that gives increased dominance status (Sundström *et al.*, 2004). Furthermore, Sundström *et al.* (2005) observed different responses of cultured and wild brown trout originating in the same stock, which may be caused by different selection regimes in the hatchery and nature (Huntingford and Adams, 2005). In coho salmon, aggression and growth rate are negatively correlated (Vøllestad and Quinn, 2003), probably because time spent on agonistic interaction reduces food consumption and/or increases energy use. Therefore, broodstock selection for production traits in hatcheries may counteract the selection for increased aggression under hatchery conditions. Hatchery broodstocks are also selected for other traits such as high age at sexual maturity (Gjerde *et al.*, 1994; Gjedrem, 2000), disease resistance (Fjælestad *et al.*, 1993; Gjøen *et al.*, 1997), feeding efficiency (Kolstad *et al.*, 2004), and low percentage of sexually mature male parr (Wild *et al.*, 1994), which distinguish farmed salmon from their wild origin with effects on their life history and survival when released into nature (Jonasson *et al.*, 1997).

Inbreeding may also occur in hatcheries with negative effects on individual and population performance when the fish are released into nature. Garant *et al.* (2005) reported an increased reproductive success of females with more mates resulting in more outbred offspring. Therefore, enhancement of offspring genetic diversity may increase the reproductive success of cultured fish when released into nature.

Ecological interaction between cultured and wild fish

Feeding competition and aggression in parr

The results of experimental tests of feeding competition between wild and cultured salmon differ. Einum and Fleming (1997) observed that parr of farmed Atlantic salmon dominated wild fish in one-on-one challenges, with hybrids exhibiting intermediate success. The authors related this to greater aggression in farmed fish, as compared with wild fish. Similar dominance of cultured fish was reported by Rhodes and Quinn (1998) for coho salmon. Furthermore, 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. On the other hand, Riley *et al.* (2005) found no evidence that rearing environments caused more aggression in cultured steelhead fry than in wild steelhead fry.

The greater aggression observed in some cultured fish populations can be modified by the environment. For example, Fleming and Einum (1997) reported that farmed Atlantic salmon parr were more aggressive in tank environments,

in contrast to the dominance of wild juveniles in stream-like environments. Moreover, Höjsjö *et al.* (2004) found that, in brown trout, the growth rate of dominant individuals relative to subordinates decreased with increased habitat complexity, lending support to the hypothesis that habitat complexity favours wild salmonids in competition with cultured conspecifics.

Prior residence also influences the outcome of competition between wild and cultured fish. In Atlantic salmon, it determines which individuals obtain territories (Cutts *et al.*, 1999). In brown trout, territory owners were more likely to win contests, whether the fish were of wild or cultured origin (Sundström *et al.*, 2003), and prior residence of 4 days motivated a stronger defence than a 2-day residence (Johnsson and Forser, 2002). Furthermore, the pre-experimental environment influenced the outcome of competition between wild and cultured juvenile salmon, and prior residence in the competition arena was important to the outcome of contests (Reinhardt *et al.*, 2001). Metcalfe *et al.* (2003) found that captive-reared Atlantic salmon were dominant over wild-origin fish in stream-tank compartments, but if the wild-origin fish were given a 2-day prior residence in the territory, the asymmetry in dominance was reversed. The relative body size of contestants had a negligible effect on contest outcomes (Huntingford *et al.*, 1990). They concluded that, although farmed Atlantic salmon were inherently more aggressive than wild-origin fish, the hatchery environment reduces their ability to compete for territories with wild resident fish in nature. Others have reported a competitive effect of size. The aggression of wild fish is suppressed by cultured salmon when they are larger than the wild fish, and this behavioural shift of wild fish may increase energy expenditure and exposure to predators when cultured fish are present in the river (Peery *et al.*, 2004).

In summary, although cultured fish may win feeding contests in tanks with slow-flowing water, the dominance can be reversed if intrinsic or extrinsic conditions change.

Migratory behaviour

When released into rivers, cultured Atlantic salmon smolts move quickly to the sea, even when released in daylight. Wild smolts usually move to the sea over a longer period, starting in cool temperature and moving downstream by night, and gradually becoming day-active as temperatures rise above ca. 13°C (Thorpe *et al.*, 1994). Wild smolts may also be entrained during the day in schools consisting chiefly of hatchery fish (Hansen and Jonsson, 1985). The large schools may shelter the fish during the seaward migration and render daytime migration more beneficial than when no cultured smolts are present. The association of wild fish in schools of cultured smolts has been termed “the Pied Piper effect” (Weber and Fausch, 2003). Zaporozhets and Zaporozhets (2004) claim that chum salmon (*Oncorhynchus keta*) behave similarly; when large

numbers are released, both cultured and wild juveniles migrate quickly to sea, and the authors suggest that this may be partly the result of intraspecific competition in fresh water, with crowding and overexploitation of the forage base.

Cultured Atlantic salmon move actively with the current in the same general direction as wild smolts, through estuaries, along the coast, and into the North Atlantic (Jonsson *et al.*, 1993a; Hansen *et al.*, 1999; Hansen and Jacobsen, 2003; Thorstad *et al.*, 2004; Lacroix and Knox, 2005), but only a small number of cultured salmon feed at West Greenland, in contrast to wild salmon (Hansen *et al.*, 1997). This may be because most cultured salmon mature after only one winter in the ocean, but only salmon that are destined to mature as multi-sea-winter fish occur at West Greenland. There are also differences in distribution between released cultured and wild salmon in the Baltic Sea, because wild fish are found more frequently in the Baltic Main Basin (Juttila *et al.*, 2003).

Mean displacement speed of wild Atlantic salmon post-smolts in a mid-Norwegian fjord was between 0.5 and 1.8 body lengths per second (Finstad *et al.*, 2005). Mean migratory distance of cultured post-smolts along the Norwegian coast has been estimated at 7.5 km per day or between 0.5 and 0.6 body lengths per second (Jonsson *et al.*, 1993a). The displacement speed of sea trout (*S. trutta*) post-smolts is more variable, between 0.1 and 2.6 body lengths per second (Finstad *et al.*, 2005). Anadromous brown trout dwell mainly in estuaries (Knutzen *et al.*, 2001, 2004; Rikardsen and Amundsen, 2005), but some long-distance migratory individuals, such as those crossing the North Sea from France to Scandinavia (Euzenat *et al.*, 1999), have been recorded.

Juvenile Atlantic salmon migrate actively through fjords into the ocean (Finstad *et al.*, 2005). Sexually maturing cultured post-smolts, on the other hand, seem more inclined to stay in coastal areas and to enter rivers as they migrate (Hansen *et al.*, 1987; Jonsson *et al.*, 1993a). Wild Atlantic salmon rarely attain sexual maturity during the first summer at sea, in contrast to cultured salmon.

When sexually mature, wild and cultured salmon enter rivers to spawn, and both may home to the area of their origin (Jonsson *et al.*, 1990, 2003a). However, cultured salmon may not originate in a specific river and may return to areas adjacent to the hatchery outflow (Clifford *et al.*, 1998). Their homing precision appears to be 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 for sea-ranched and wild Atlantic salmon of the River Imsa stock were estimated at 15% and 6%, respectively, when both types of fish left the river as smolts in May. Moreover, the straying rate was higher for Atlantic salmon attaining sexual maturity and returning to fresh water after two years at sea rather than one year. The longer the time fish stayed away from their home river, the greater the chance of straying. Both cultured and wild salmon

strayed to many of the same rivers, ca. 80% of which drain into the fjord of the River Imsa within 60 km of the outlet. Therefore, the chance of entering the “wrong” river increases with time or distance moved at sea.

Farmed post-smolt salmon that escape to sea in winter do not return to any specific area when sexually mature (Hansen and Jonsson, 1991), and fish released when maturing in their second summer also appear to have lost their ability to navigate back to their home river or place of release (Hansen *et al.*, 1987). There is probably a finite period when Atlantic salmon are able to choose navigational cues that they use during the return migration. Sub-adults and adults have lost this ability (Hansen *et al.*, 1993; Hansen and Jonsson, 1994). Therefore, many cultured fish may reproduce in rivers other than the one that they left as smolts.

In summary, the migration pattern of wild and cultured salmon is similar, but there are some differences in their respective marine distributions, and homing precision is quite different.

Marine feeding

Anadromous salmonids obtain most of their resources at sea, although the specific rate of seasonal growth may be no higher than in fresh water (Jonsson and Jonsson, 2003). Atlantic salmon post-smolts feed opportunistically on pelagic prey, and the prey species change along the migratory route from the coastal habitat to the open ocean (Lacroix and Knox, 2005). In the Bay of Fundy and Gulf of Maine, post-smolts feed largely on amphipods and, thereafter, on krill (Euphausiacea) and fish. In the Baltic Sea, post-smolts feed largely on surface insects during summer, but at lengths between 24 and 32 cm, they change to piscivory, with herring as their main food (Salminen *et al.*, 2001).

In the North Atlantic, cultured post-smolts have considerably more food items in their stomachs, especially amphipods and krill, than do wild post-smolts. Amphipods were the most abundant item in the stomachs of cultured post-smolts, whereas krill was the most abundant food item of wild post-smolts. Fish, mostly sandlances (Ammodytidae), the largest prey item consumed, were almost twice as abundant in the diet of cultured post-smolts as in that of their wild counterparts. In the northeastern Atlantic, mesopelagic fish such as lanternfish (Myctophidae), pearlsides (Sternopychidae), and barracudinas (Paralepididae) were more important than amphipods, which were more important than krill (Jacobsen and Hansen, 2001). In the open ocean, the diet of wild and cultured salmon is similar, indicating that cultured fish are well adapted to ocean life.

Few studies have investigated feeding competition between wild and cultured salmon in the ocean, but there may be localized exploitative competition between cultured and wild salmon. For example, Hilborn and Eggers (2000) attributed the decline in stock abundance of wild pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound to feeding competition with the many cultured fish

present. They concluded that hatchery production has largely replaced wild fish. Wertheimer *et al.* (2004a), on the other hand, concluded that wild salmon production there is driven primarily by density-independent marine conditions, but that the release of cultured fish has contributed to the decline in body size because of density-dependent growth. However, the survival rate may decrease as an effect of slower growth, as for other Pacific salmon (Beamish and Mahnken, 2001; Beamish *et al.*, 2004a). There is also reason to believe that such competitive interaction can occur in Atlantic salmon, in areas with high densities of cultured fish.

Spawning

Cultured Atlantic salmon enter rivers to spawn later in the season, move about more, and stay in the river for a shorter time than wild fish (Jonsson *et al.*, 1990; Økland *et al.*, 1995). That cultured fish are not homing to any particular spawning area, probably influences upstream migration. Many of them move to the top of the river instead of entering the spawning grounds of wild fish lower downstream (Thorstad *et al.*, 1998). Some cultured salmon spawn in the river they enter, while others leave without spawning (Jonsson *et al.*, 1990). The spawning success of cultured salmon may be reduced by late river entry (Aarestrup *et al.*, 2000).

On spawning grounds, cultured fish are competitively and reproductively inferior and are injured more often than their wild counterparts (Jonsson *et al.*, 1990; Fleming *et al.*, 1996, 1997). For non-native Atlantic salmon, McGinnity *et al.* (2004) reported that overall lifetime success from fertilized egg to returning adult is 35% less than that of native and ranched conspecifics. In a “whole river” experiment, Fleming *et al.* (2000) found that farmed adults achieve less than one-third of the breeding success of native salmon. Early survival was less in offspring of cultured fish than that of wild fish, but subsequently, it was similar. In this experiment, farmed fish depressed the native production by more than 30%, and the lifetime reproductive success of the farmed fish was 16% that of the native salmon. The inferiority of cultured fish was sex-biased, being more pronounced in males than in females and resulting in cross-breeding between cultured females and wild males. Studies in an experimental stream indicated that cultured brown trout males appear to have less reproductive success than wild males, but a similar effect was not found for females (Dannewitz *et al.*, 2004).

Experimental evidence from Atlantic salmon suggests that the difference in fitness results from cultured females being morphologically maladapted (Fleming *et al.*, 1994; Gross, 1998), being less active, displaying less breeding behaviours, constructing fewer nests, retaining a greater mass of eggs unspawned, incurring more nest destruction, being less efficient at nest covering, and suffering greater egg mortality than wild females. Farmed males do not establish

dominance hierarchies as effectively as wild males, court less, spawn with females in larger numbers and participate in fewer spawnings, and frequently fail to release sperm when the females release their eggs. Experimental evidence suggests that they achieve only a low percentage of the reproductive success of wild males (Fleming *et al.*, 1996; Weir *et al.*, 2004, 2005). In rivers, however, sexually mature male parr can fertilize eggs even if the large adult males are inactive (Garant *et al.*, 2003; Weir *et al.*, 2005). In other salmonids such as coho salmon, reproductive success is greater for wild than for cultured fish (Fleming and Gross, 1992, 1993; Berejikian *et al.*, 1997). However, the reproductive success of cultured fish may increase as time spent in nature increases. For example, the reproductive success of sea-ranched salmon that have lived for one year in nature is between that of wild salmon and farmed Atlantic salmon taken directly from net pens (Fleming *et al.*, 1996, 1997).

The time in hatcheries may not always decrease the reproductive success of cultured salmon. Dannewitz *et al.* (2004) found no significant difference in reproductive success between seventh-generation cultured trout and wild brown trout in an experimental stream. Therefore, cultured fish are not always competitively inferior to wild fish on the spawning grounds, indicating that supportive breeding can be managed to increase the effective population size of endangered salmonid populations.

Ecological significance of interaction

In addition to genetic effects such as those caused by cultured fish introgressing wild gene pools (Fleming *et al.*, 2000; Utter, 2004), cultured salmon influence wild populations in many ways. These include increasing their emigration and mortality, decreasing their growth rate, biomass, and production, and altering their life history traits (Figure 1).

Emigration

Releases of cultured fish may displace wild conspecifics, as McMichael *et al.* (1999, 2000) found in experiments with rainbow trout. Weiss and Schmutz (1999) observed the movement of resident trout from stocked stream sections. Whether cultured fish dominate wild conspecifics will probably vary according to their genetic background. In their review, Weber and Fausch (2003) presented examples from experiments in which nearly equal proportions of cultured and wild adult brown trout dominated in experimental encounters. There are also examples of cultured salmon having no effect. For example, Orpwood *et al.* (2004) reported that the ability of wild Atlantic salmon parr to find shelter in winter was unaffected by the presence of cultured parr, even when the wild fish were outnumbered four to one.

When the effects of competition among cultured and wild chinook salmon were studied in laboratory channels, it was

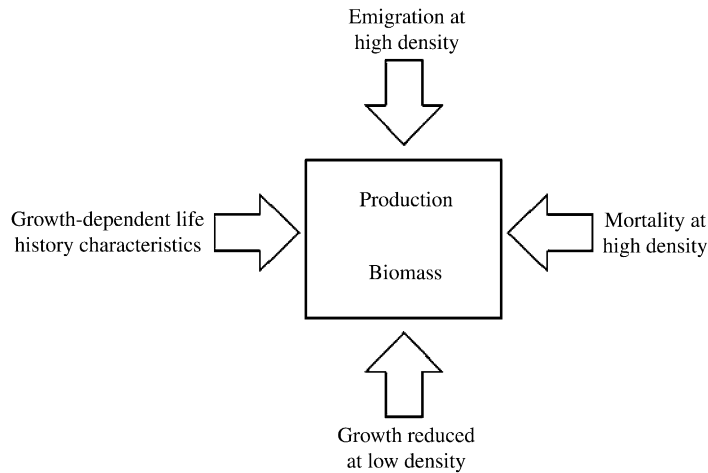


Figure 1. Density-dependent, ecological changes in production and biomass of wild salmonids resulting from the release of hatchery conspecifics. See text for detailed explanation.

observed that the displacement of wild fish may be linked to body size and fish density. Weber and Fausch (2003) reported that, at high density, cultured fish were able to displace wild fish from favourable stream positions when the cultured fish were larger. At normal density, however, no consistent effect on emigration was found.

Mortality

A habitat's carrying capacity is limited (Einum and Nislow, 2005). Studies on stock-recruitment relationships suggest that salmonid populations are regulated by density-dependent mortality during early life stages after fry emerge from the spawning gravel. 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 there are also exceptions of density-dependent mortality at later stages (Unwin, 1997; Elliott and Hurley, 1998).

Density-dependent mortality can result from releases of cultured fish. For example, McGinnity *et al.* (1997) reported that cultured Atlantic salmon fry outgrew and partly replaced wild conspecifics. Nickelson *et al.* (1986) found that the density of wild coho salmon juveniles was less in streams stocked with cultured fish than it was in unstocked streams, indicating that cultured fish replace wild fish. The total density of juveniles had increased one year after stocking, but production of juveniles decreased in the next generation. Nielsen (1994) reported reduced production of wild coho salmon after cultured coho salmon were stocked in a Californian river. Vincent (1987) found that densities of wild rainbow trout and brown trout increased after stocking of adult cultured rainbow trout ceased in two Montana streams, and Petrosky and Bjornn (1988) found that the mortality of wild rainbow trout and cutthroat trout (*Oncorhynchus clarki*) increased at high, but not at low, stocking

densities. In competition experiments with masu salmon in river enclosures, cultured fish survived in larger numbers than wild fish (Reinhardt *et al.*, 2001). Bohlin *et al.* (2002), who tested the effects of competition from cultured brown trout on wild conspecifics, reported that the mortality effect of released cultured fish may be similar to that of adding wild fish. Therefore in fresh water, density-dependent effects of cultured fish appear common among salmonid species.

Releases of cultured fish may also influence other competing species. For example, Levin and Williams (2002) reported that the survival of wild chinook salmon is negatively associated with releases of cultured steelhead trout into the Snake River, and similarly, releases of Atlantic salmon influence the carrying capacity for brown trout as a result of competitive interaction (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 the intraspecific competition between cultured and wild Atlantic salmon. The different salmonid species are opportunistic feeders and can adapt their feeding behaviour to their social environment, and although their ecological requirements may be similar, they are less similar than are those of cultured and wild salmon (Harwood *et al.*, 2002).

Less is known about the effects of cultured Atlantic salmon on other salmonid species when they occur outside their native range. In some cases effects may be negative, such as the effect of released brown trout on native salmonids, including white-spotted charr (*Salvelinus leucomaenis*) and masu salmon in Hokkaido, Japan (Hasegawa *et al.*, 2004). In other cases, the negative effects may be less because: (i) the species may have different feeding requirements, (ii) Atlantic salmon have difficulty in establishing self-sustaining populations beyond their native range (Volpe *et al.*, 2000), and (iii) the released fish may be

subordinate to the species already present (Scott *et al.*, 2003, 2005). The effects of released cultured salmon on other ecosystem components have rarely been studied, but they may restructure local foodwebs (Waknitz *et al.*, 2003; Baxter *et al.*, 2004).

Growth

Density can influence salmonid growth rate (Brännäs *et al.*, 2005). Whereas density-dependent mortality is strongest at high population densities, density-dependent growth appears strongest at low population densities (growth depensation; Jenkins *et al.*, 1999; Lobon-Cervia, 2005). Growth depensation caused by the release of cultured fish has been observed in Atlantic salmon (Imre *et al.*, 2005) as well as in brown trout and rainbow trout, and probably occurs in salmonids generally (McMichael *et al.*, 1997, 2000; Weiss and Schmutz, 1999; Sundström *et al.*, 2004). Bohlin *et al.* (2002) found that the addition of cultured trout had an effect on the growth of wild brown trout that was similar to that of increasing the density of wild fish. A consequence of growth reduction may be decreased survival and an influence on other life history traits (Beamish *et al.*, 2004b; Jonsson and Jonsson, 2004).

Other life history traits

The release of cultured salmon can contribute to a decline in adult body size in locations where the fish are released as a result of feeding competition and because hatchery practice with rapid juvenile growth in freshwater often results in younger age at maturity as a phenotypic response (Salminen, 1997; Quinn *et al.*, 2001; N. Jonsson *et al.*, 2003; Vøllestad *et al.*, 2004; Scheuerell, 2005). Furthermore, broodstock selection for early age at maturity can occur in Pacific salmon because it is simpler and less time consuming to handle smaller fish (Unwin and Glova, 1997). In farmed Atlantic salmon, on the other hand, broodstocks are usually selected for high age at maturity (Gjerde *et al.*, 1994), because maturation is energy-consuming and reduces meat quality.

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 in fresh water, as it occurs in hatcheries, reduces egg size and increases fecundity as a plastic response of the phenotype, whereas the effect of growth-rate variation on egg size at sea is minimal (Jonsson *et al.*, 1996), a correlation that also holds for masu salmon (Tamate and Maekawa, 2000). Variation in growth rate, adult size, age at maturity, egg size, and fecundity influences competitive ability, reproductive success, and fitness, with effects on biomass and production of fish in nature (Wertheimer *et al.*, 2004b). In salmonids, adult size is the main determinant of fecundity (Thorpe *et al.*, 1984; Jonsson and Jonsson, 1999).

Biomass and production

Releases of salmon (alevins, parr, and smolts) are intended to increase the productivity of habitats, but hatchery production may decrease the productivity of the wild stock present. Fleming *et al.* (2000) reported a 30% reduction in wild production of Atlantic salmon in a Norwegian river, and Unwin and Glova (1997) found a 34% reduction of chinook salmon stocked in a New Zealand stream, probably the result of density-dependent mortality of wild fish. Moreover, Nickelson (2003) reported decreased production of coho salmon in Oregon coastal river basins and lakes, where large numbers of cultured smolts were released. Based on his findings that populations composed of equal numbers of cultured and wild fish produced 63% fewer recruits per spawner than one composed entirely of wild fish, Chilcote (2003) maintained that removal, rather than addition, of cultured fish may be the most effective strategy for improving productivity and resilience of steelhead trout. Cases in which fish releases cause a decrease rather than an increase in total population size may be the result of a genetic change, with the introduction of maladaptive traits or loss of genetic variation (Wang and Ryman, 2001), or an overexploitation of the available food resources, with a consequent decrease in the habitat's carrying capacity. In cases reported by Hayes *et al.* (2004), only minor effects of released cultured fish on the local wild populations appeared. However, when Goodman (2005) modelled the effects on natural spawning fitness in rivers where wild and cultured fish spawned together, he found that natural spawning fitness may be eroded, a finding supported by the analysis of Naylor *et al.* (2005). Therefore, results varied, from decreased to increased total production after releases of cultured salmon, findings that are reasonable and dependent on the environmental conditions in the area where the fish are liberated.

Further research

Whether the objective is to enhance salmonid river production or to protect wild stocks from escaped fish, we need better knowledge of how hatchery conditions change the fitness of cultured fish in nature. This will facilitate improved management of hatcheries producing fish for farming or for release into nature. In particular, we need more knowledge on the plasticity of genotype–environment interaction. For example, we know that the velocity of the current influences hormonal changes, with effects on behaviour, growth, and life histories of salmonids (McCormick *et al.*, 2003), and that elevated egg incubation temperature influences subsequent metabolic and growth rates (Rungruangsak-Torrissen *et al.*, 1998, 1999), with possible effects on age and size at smolting and sexual maturity (Jonsson *et al.*, 2005). We lack, however, a quantitative understanding of how important these changes are to factors such as maximum growth rate, optimal temperature and temperature

limits for growth, and life history characteristics associated with growth rate through norms of reaction. It is generally assumed that, although age at maturity decreases with increased growth rate, adult size first increases and then decreases with increasing age at first maturity (Alm, 1959). Berrigan and Charnov's (1994) hypothesis – that ectotherms mature older but at a smaller size when growth rates are reduced by a reduction in food quality, and that they mature later, at a larger size, when growth rate is lowered by a reduction in temperature – is relevant in this context. It could be tested in controlled hatchery experiments and through the release of cultured fish into nature. Such knowledge would be helpful in both the management of the release of cultured fish and in the understanding of animal demography by life.

The velocity of the current in hatchery tanks is usually lower than that experienced by wild Atlantic salmon parr, inducing a number of hormonal differences (Youngson and Webb, 1992; Iwata *et al.*, 2003; McCormick *et al.*, 2003). For example, lower levels of thyroxine in cultured smolts may influence anadromous migration by affecting the learning of stream odours for use in subsequent homing (Dittman *et al.*, 1996) and river ascent for spawning (Jonsson *et al.*, 1994; Skilbrei and Holm, 1998). Improved understanding of the relationships among environmental variables, hormonal levels, and subsequent behavioural performance would help in the management of smolt production for release into nature.

Experimental evidence suggests that aggressive cultured fish can outcompete wild offspring and decrease their productivity in rivers (Fleming *et al.*, 2000), but more research is needed to determine the generality of such results. Research on spawning competition between wild and cultured salmon has progressed considerably since it began approximately 20 years ago. Still needed, however, is enhanced knowledge of the long-term effects of cultured fish in nature and of factors influencing the resilience of natural populations against a continuous and massive immigration of farmed conspecifics. New research in this field should focus on the effects of cross-breeding between the two and the possible effects of transgenic and developmentally manipulated fish. Natural selection may rapidly eliminate maladapted traits as indicated by findings about Pacific salmon (Quinn *et al.*, 2001; Kinnison and Hendry, 2004), but a continued high immigration rate of cultured fish into wild populations may have long-term effects.

Mortality of cultured salmon in nature is often very high. This is probably the result of the changed performance of the fish, stemming from a phenotypic change caused by the juvenile rearing environment (Dannewitz *et al.*, 2003). More research is needed to explain why this occurs and how hatcheries can be managed to avoid such high mortality of cultured salmon in nature.

Most research on cultured salmon concerns the effects on conspecifics. There is, however, growing concern about the effects of cultured salmon on the ecosystem, especially

outside the native range of the species. Like rainbow trout in Europe (Jonsson *et al.*, 1993b), Atlantic salmon colonize poorly and have failed generally to establish self-sustaining, anadromous populations beyond their native range when released elsewhere (Naylor *et al.*, 2005). However, because their current range represents colonization after the last glaciation period, they are not ineffective colonizers in principle, and escaped farmed salmon compete with and prey upon the native fauna wherever they occur. They have the potential to restructure local foodwebs (Pascual *et al.*, 2002; Waknitz *et al.*, 2003; Baxter *et al.*, 2004; Scott *et al.*, 2005). Further research is needed to evaluate this risk.

Little is known about the consequences of cultured salmon at sea, but massive escapements from fish farms may have substantial effects. Cultured fish consume food resources at rates similar to those of wild fish (Jacobsen and Hansen, 2001), and escapees increase resource competition with possible density-dependent effects. A few studies of the Pacific Ocean have focused on this issue (Hilborn and Eggers, 2000; Wertheimer *et al.*, 2004a), but virtually nothing is known about this in the Atlantic Ocean, although the impact of cultured salmon on natural ecosystems may be considerable.

Conclusions

- (i) Cultured salmon compete for food, space, and breeding partners with wild conspecifics in nature.
- (ii) Their performance and reproductive success in nature are variable, but can be much poorer than those of wild conspecifics of similar size.
- (iii) Reduced fitness is the result of the morphological, physiological, ecological, and behavioural changes that occur in hatcheries. These changes are partly short-term phenotypic adjustments resulting from the changed environment and partly long-term adaptations with changed gene frequencies caused by broodstock selection and differential mortality.
- (iv) The success of cultured fish increases with the amount of time spent in nature. The performance may be increased by modifications to the hatchery environment, such as temperature adjustment and increased water flow.
- (v) Through density-dependent mechanisms, cultured fish in nature may displace wild fish to some extent, increase their mortality, and reduce their growth rates with effects on the associated life history traits, biomass, and production.
- (vi) Important research topics to be put in hand are the study of factors influencing the performance of cultured fish in nature and the ecosystem effects of increased salmon abundance in fresh- and saltwater inside and outside the original range of the species.

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