

# The Ability of Released, Hatchery Salmonids to Breed and Contribute to the Natural Productivity of Wild Populations

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## Abstract

The success and implications of hatchery release programmes are intimately tied to the reproductive capabilities of the hatchery fish in the wild. Moreover, reproductive interactions are important in understanding the ecological and genetic threats that hatchery fish may pose to wild populations. Reproductive success is a key to self-sustainability, shaping natural and sexual selection, and influencing the genetic diversity of populations. In this paper, we review the determinants of breeding success in natural populations and the implications of parental traits and decisions for offspring survival and success. We then address how rearing and release programmes affect the reproductive traits and performance of fish. A review of such programmes reveals that in the few cases where adequate assessments have been made released fish frequently fail to attain self-sustainability and/or contribute significantly to populations. Clearly, new approaches based on sound scientific research are needed and these need to be tailored specifically to the management objectives.

Keywords: hatchery, salmonids, natural productivity, breeding success, spawning.

## Introduction

Deliberate releases of salmonid fishes appear to take two main forms: (1) *fisheries releases* to increase population size for fisheries; and (2) *conservation releases* to save populations at risk of extinction or re-establish native populations that have been eradicated. Fisheries releases are the most common and in Norway, are most often undertaken for mitigation purposes, i.e. to compensate for the impacts of habitat alteration/degradation such as hydropower regulation (Finstad and Jonsson 2001, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001). An unfortunate consequence of this approach is that it can become acceptable to sacrifice the productivity of natural populations as long as the hatchery re-

leases compensate for the loss to the fisheries. Little consideration is given to habitat or other improvements. This approach is also problematic because hatchery fish are often stocked on top of the natural production, which has become constrained by habitat loss (i.e. reduced natural carrying capacity), thus inducing potentially deleterious competition between the wild and released fish (reviewed in Einum and Fleming 2001, Sægrov et al. 2001). Only recently have we begun to fully appreciate that the long-term sustainability of salmonids requires conservation of natural populations and their habitats.

Conservation releases are often undertaken to save populations that are likely to perish due to demographic factors (e.g., small population size). Such releases aim to use native fish as broodstock

to give the population a boost (supportive breeding) and in theory, are to be considered a temporary solution until the factors responsible for the population decline are identified and alleviated. Conservation releases may also be undertaken to re-introduce/re-establish populations that have been eradicated (e.g., because of acid rain or the parasite *Gyrodactylus salaris*). Once the cause of the extinction has been rectified, fish are re-introduced either from the population's gene bank or from neighbouring populations inhabiting similar environmental conditions, i.e. having adaptations likely to aid in establishment.

One of the main premises/goals upon which many of the above concepts of fish releases are built upon is that they can provide a positive long-term benefit to natural populations. Yet, there appears to have been little or no attempt to find out whether this goal is achieved, and this is not a problem restricted to Norway, but a universal problem (cf. Waples et al. in press). Thus, the role of fish releases in the conservation of wild salmon populations is intimately linked to understanding the dynamics of breeding and ultimately, reproductive success between wild and hatchery released salmon. The aim of the paper is to review the determinates of breeding success and its close link with offspring success (reproductive success) in salmonid fishes, particularly Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*). Then we examine the close relation between reproductive success and the desired goals of release programs, and how they may affect the reproductive traits and performance of fish. Finally, we provide an analysis of release programs where direct and indirect information about the reproductive success of released salmonids and their potential effect on natural productivity exist.

## Demographic and genetic consequences of breeding success

Breeding success is the outcome of competition among individuals to maximise the number of embryos surviving until independence (i.e. yolk

absorption in salmonids) within the constraints imposed by the opposite sex (e.g., number of mates, mate choice) and the environment. Because of its link via offspring survival to individual reproductive success (a measure of fitness), it plays an important role in shaping the demographic and genetic structures of populations (cf. Vehrencamp and Bradbury 1984).

From the population perspective, the most obvious implication of variation in breeding success is its effects on annual recruitment and thus natural production. However, natural breeding also generates intense selection upon both male and female salmon that shapes life history strategies and thus the demographic structure of populations. Evidence from a series of semi-natural breeding experiments with Atlantic salmon (Fleming et al. 1996, 1997) indicate that breeding alone can generate a coefficient of variation in female success of 102% (range 71-131%) and in male success of 151% (range 60-268%). Thus, the variance in breeding success is often considerably larger than the mean success, with some individuals being highly successful while others are unsuccessful (range in female success: 0-4,644; male success: 0-11,188 embryos parented). This generates intense natural and sexual selection on male and female salmonids targeting traits such as body, hooked snout, kype, dorsal hump, caudal peduncle, and adipose fin size (van den Berghe and Gross 1989, Järvi 1990, Fleming and Gross 1994, Quinn and Foote 1994, Petersson et al. 1999). It also affects life history traits, including survival, egg production, age at maturity and the evolution of alternative reproductive tactics (e.g., sneaking versus fighting), and subsequently the demographic features of the population such as sex ratio and age structure (reviewed in Fleming 1998). Any program to conserve salmonid populations, therefore, must take account of the variation in breeding success, particularly when hatchery release programmes are being considered.

Variability in breeding success of individuals also affects the genetic structure of populations in subsequent generations, both directly through selection as described above and indirectly through its effects on a population's effective

size. The effective size of a population ( $N_e$ ) is an important parameter determining the amount of genetic variability that can be maintained, particularly when the population is small (e.g., Martinez et al. 2000). It is defined as the size of an ideal population that would lose genetic variation at the same rate as a given real population (Lande and Barrowclough 1987). The loss of genetic variability influences the population's probability of long-term survival because genetic variation is requisite for evolutionary adaptation in changing environments. Things that affect  $N_e$  include variability in population size through time, skewed sex ratios and variability among individuals in breeding success (Lande and Barrowclough 1987, Nunney 1991). Variability in breeding success in salmonids can reduce the breeding effective size to 48-76% of the number of adults on the spawning grounds (Fleming 1994, cf. Nunney and Elam 1994).

Populations will often go extinct due to demographic problems (stochastic and/or deterministic) before loss of genetic variability can become a problem (Lande 1988). Thus demography will often be a more pressing conservation problem than genetics, though genetic diversity will remain important in maintaining the potential for adaptive evolution. Two forms of variability will affect the demography of populations at small sizes, demographic (e.g., sex ratio, age-structure) and environmental (e.g., weather, food supply, competitors, parasites). They are generally overlapping categories to describe different forms of variation that influence the demography (i.e. survival and reproduction) of a population. Environmental variability is considered to pose a greater threat to population survival (Lande 1988, 1993, Caughley 1994). Analyses by Leigh (1981) and Goodman (1987) suggest that environmental variability will usually dominate other forms of variability in populations larger than 20-100 individuals. In most real situations we are likely to have environmental variability first driving populations to low levels and demographic and genetic variability then putting on the finishing touches. The central message is that risk of extinction increases with decreasing population

size and will be affected by variation in breeding success.

A final aspect where breeding success plays a critical role is in understanding the potential for gene flow. In the present context, such gene flow will frequently be one-way from cultured to native fish, though some supplementation programs will obtain a fraction of their broodstock from the wild each generation. If interbreeding is successful, the resultant gene flow may lead to the loss of genetic variability among populations, an important component of genetic variation in salmonid species and their evolutionary potential (e.g., Ståhl 1987, Allendorf and Leary 1988, Waples 1991, Hansen and Loeschcke 1994). At the within-population level, however, the effects may be negative or positive. Interbreeding may disrupt local adaptations and break up coadapted gene complexes (i.e. combinations of genetic traits that have evolved over a long period to work complementarily) resulting in a reduction in fitness known as outbreeding depression (Templeton 1986). By contrast, it may simultaneously increase genetic variability, thereby reducing the accumulation of recessive deleterious mutations in populations suffering from inbreeding depression, and increasing within-population evolutionary potential. Despite such potential positive effects, Hindar et al. (1991) in a review of intentional (e.g., transplants) and unintentional introductions of salmon (e.g., salmon farm escapes, straying of hatchery releases) found that the effects were frequently negative (see also Gharrett and Smoker 1991).

## What determines breeding success?

Mating success is one of the most important factors determining breeding success. If an individual were not able to achieve matings, its reproductive output would be zero, whatever qualities the individual has in other respects. But, an ability to achieve matings does not necessarily translate into breeding success (e.g., due to low gamete viability or poor embryo survival). Breeding success in salmonid fishes will be determined by

a variety of factors, such as body size, timing, egg production, competitive ability, attractiveness, and embryo viability. The theoretical underpinnings to understanding investments in these various traits assume that different life history components are causally related and increases in allocation to one component, for example reproduction, will be at the expense of allocation to other components, such as growth and survivorship (Williams 1966, Gadgil and Bossert 1970). However, such trade-offs may be masked in the wild because of individual variation in the ability to acquire resources, with individuals having better acquisition abilities being able to devote more energy into a wide array of traits (Reznick et al. 2000). In this section we aim to review some important elements of breeding success and how they are interrelated.

### Age and size at maturity

Age and size are coupled in most fish species, with older individuals being generally larger than younger ones. In organisms having indeterminate growth, such as fish, the relation between growth and reproduction is potentially very important because size and fecundity are often positively related. In terms of lifetime reproductive potential, early-breeding individuals may maintain a higher cumulative reproductive output until a certain age; after which late-breeding individuals may have a higher cumulative potential (cf. Ford and Seigel 1994). This reflects the decreased growth often associated with increased reproductive investment that reduces future fecundity (cf. Williams 1966). Also, maturing at young age provides a demographic benefit in terms of decreasing generation times in expanding populations, while delaying breeding incurs an accumulated risk of dying (e.g., due to diseases, parasites, predators or senescence) (Bell 1980). Thus, the optimal size-to-age at maturity depends on growth and mortality rates, which vary with environment (Charlesworth 1980). Therefore, organisms in spatially or temporally changing environments frequently show adaptive phenotypic plasticity for this trait (Schlichting and Pigliucci 1998).

Early experimental work by Alm (1959) showed

that a dome-shaped norm of reaction for size-to-age at maturity is common in fishes, with size at maturity being smaller for both fast- and slow-growing individuals than for more intermediate-growing fish. Using computer simulations, Perrin and Rubin (1990) showed that such a dome-shaped norm of reaction is optimal when assuming a finite life span and a negative relationship between production and survival rates. This latter assumption is supported by empirical data (e.g. Beverton and Holt 1959, Jensen 1985), as well as by physiological and demographic arguments (e.g. Sibly and Calow 1986). Age and size at which to mature are then among the principal components of the reproductive strategy (i.e. a genetically based life history or behaviour programme affecting an organism's allocation to reproductive effort among alternative phenotypes or tactics; Gross 1984, 1996) of a salmonid species.

Considerable variability in these traits exists among and within species, and also among and within populations of a species, including salmonid fishes (e.g., Alm 1959, Jonsson 1985, Groot and Margolis 1991, Hutchings and Jones 1998). In addition to the effects of abiotic conditions, this variability in salmonid fishes is influenced strongly by reproductive success as affected by the breeding environment (reviewed in Fleming 1998), and by the costs of reproduction (e.g., survival; Hutchings 1994). One of the most striking examples of this occurs within Atlantic salmon and brown trout, where some males mature during their freshwater stage as parr while others mature after an oceanic migration. The mature male parr may be less than a hundredth the weight, and about a third the age of ocean-migratory (anadromous) males (Fleming 1998). These two male phenotypes appear to coexist as a result of the combined effects of frequency- and status-dependent selection during breeding (Gross 1984, 1996, Bohlin et al. 1986, 1990, Hutchings and Myers 1994), where the relative success gained from using a particular tactic (anadromy versus parr maturity) will be influenced by an individual's competitive ability ("state") and the tactic used by others in the population.

## Intrasexual competition

In most salmonid species, competition among individuals of the same sex for breeding resources is intense. Moreover, because males and females fight over different resources, access to females and spawning sites respectively, the intensity of intrasexual competition differs between the sexes. The operational sex ratio (OSR, i.e. the number of sexually active males to that of sexually active females on the spawning ground) is a good predictor of contest competition for mates and to some extent mate choice. However, it will not necessarily be a good predictor of the prevalence or intensity of other mechanisms of sexual selection, such as sperm competition, infanticide or coercion (see Kvarnemo and Ahnesjö 1996). In salmonids, the OSR is highly male biased in most cases (e.g., Quinn et al. 1996). Even though the sex ratio of returning adults in some cases may be female biased (Fleming 1998), the OSR (i.e. the sex ratio on the spawning grounds) is likely to be male biased. This is a consequence of (1) asynchronous spawning by females and the male ability to spawn rapid and repeatedly; for example, female Atlantic salmon may be active on the spawning ground for 7-10 days, while males may remain so for about a month (Webb and Hawkins 1989, Fleming et al. 1996, 1997; see also Blanchfield and Ridgway 1997), and (2) the presence of early maturing male parr. It is not uncommon in salmonids to observe ten or more males, including mature parr, competing for access to a single female (Keenleyside and Dupuis 1988, Evans 1994; personal observations of wild Atlantic salmon).

Evidence from coho salmon (*Oncorhynchus kisutch*) suggests that male breeding competition can generate a 52-fold increase in the opportunity for selection (Fleming and Gross 1994). Such intense selection has likely been responsible for the evolution of elaborate secondary sexual characteristics (i.e. developed for accessing breeding resources, including mates and spawning sites), such as elongated jaws and canine-like breeding teeth, dorsal humps, bright breeding colouration and skin thickening (Schroder 1982, Järvi 1990, Fleming and Gross

1994, Quinn and Foote 1994, Petersson et al. 1999). Moreover, the studies above indicate that males are more intensively selected than females. For example, Fleming and Gross (1994) found the intensity of selection due to breeding competition to be nine times greater in male than female coho, suggesting that this was responsible for the sexual dimorphism in the expression of secondary sexual characters. Such sexual dimorphism is common in salmonid fishes.

This is not to suggest that breeding competition among females is weak, but rather less intense than that among males. While breeding sites in many rivers may appear non-limiting, females do show strong preferences for particular sites, often clumping nests in such areas (Heggberget et al. 1988, Blanchfield and Ridgway 1997, Essington et al. 1998). Competition over breeding sites can result in delays in breeding, female displacement and nest destruction by superimposition (e.g., Schroder 1981, van den Berghe and Gross 1989, Fleming 1996, Petersson and Järvi 1997, McPhee and Quinn 1998, Essington et al. 2000). Fleming and Gross (1994) found that female breeding competition generated a 6-fold increase in the opportunity for selection among female coho salmon (see also van den Berghe and Gross 1989). Thus intrasexual competition in both sexes will be important in determining breeding success, and ultimately the demographic and genetic structure of salmonid populations.

## Mate choice

Empirical and theoretical data pinpoint what most biologists intuitively know, that female mate choice is much more common than male mate choice (reviewed in Andersson 1994). In salmonid fishes, females appear to express mate choice through delays in breeding (Schroder 1981, Foote and Larkin 1988, Foote 1989, de Gaudemar et al. 2000) and aggression, sometimes directing a large proportion of their aggressive activity towards males (e.g., Keenleyside and Dupuis 1988, Fleming et al. 1997, Petersson and Järvi 1997). The choice criteria of female salmonids are still relatively unstudied, with the exception of experi-

ments by Petersson et al. (1999) and de Gaude-  
mar et al. (2000) showing female choice of males  
with relatively large adipose fins in brown trout  
and large body size in Atlantic salmon, respec-  
tively. It is unlikely that female salmonids gain  
direct, material benefits from such mate choice  
(e.g., territories, food, parental care), although  
they may gain genetic benefits for their offspring  
(e.g., 'good genes' or 'runaway' coevolution; see  
Andersson 1994), safety from disruption and in-  
jury during spawning, reduced risk of infection  
and assurance of fertilisation (see Reynolds and  
Gross 1990). Recent evidence suggests males may  
also affect egg swelling immediately following  
fertilisation, which may be a special case of 'male  
contribution' (Pakkasmaa 2000, cf. Seppä 1999),  
though its significance remains unclear and un-  
studied. The extent of female choice in salmo-  
nids, however, appears to be constrained or cir-  
cumvented by male-male competition, because  
dominant males can monopolise access to fe-  
males (Jones 1959, Järvi 1990, Fleming et al. 1996,  
1997, Petersson et al. 1999). Female incitation of  
male-male competition, however, may be viewed  
as a means of 'passive' choice (cf. Cox and Leb-  
oeuf 1977), though its role in salmonid fishes is  
unstudied. The costs of the female choice in terms  
of energy, predation risk and aggression from  
males may often outweigh its benefits for salmo-  
nid fishes and as a result it is unlikely to play a  
dominant role in the mating system.

Mate choice by male salmonids is probably  
even less well studied than that of females. Males  
may show choice either for absolute female size  
because of its direct relation with female quality  
(e.g., fecundity, egg size and parental care abil-  
ity; Sargent et al. 1986) or for similar-sized females  
because of the male's ability to obtain and con-  
trol mates (Foote 1988). It is common for the  
number of males associated with a spawning fe-  
male to increase with her size (Hanson and Smith  
1967, Campbell 1977, Jonsson and Hindar 1982,  
Sargent et al. 1986). Asynchronous spawning by  
females in some circumstances, however, may  
constrain male mating options.

One possible outcome of the combination of  
mate choice and intrasexual competition is  
assortative mating, where males and females in a

population mate more frequently with a pheno-  
type (in a broad sense) similar to their own than  
expected from random. Assortative mating may  
arise when individuals of both sexes actively  
choose a mate of a similar phenotype (Burley  
1983). The rapid phenotypic and genetic diver-  
gence of Icelandic Arctic char may be an example  
of this (cf. Gíslason et al. 1999). Alternatively,  
assortative mating may arise when all individu-  
als of one sex have the same preference, but only  
some of them are able to achieve it (Burley 1983).  
For example, if all females prefer large males and  
all males prefer larger, more fecund females, then  
only the larger males are able to gain access to  
the preferred females. The smaller males and fe-  
males, as a result, will be forced to mate with each  
other (cf. Petersson 1990). This pattern is most  
likely operating in Dolly Varden (Maekawa et  
al. 1993) and Japanese charr (Maekawa et al. 1994).  
Several other studies also report positive size-  
assortative mating in salmonids (Hanson and  
Smith 1967, Schroder 1981, Jonsson and Hindar  
1982, Foote 1988). It has also been suggested  
that negative assortative mating based on major  
histocompatibility complex (MHC) genes may be  
important in salmonids, though this remains un-  
tested (Grahn et al. 1998). Assortative mating is  
likely to be a common pattern in salmonid fishes.

### The link between adult reproductive traits and offspring success

Most of the factors contributing to embryo sur-  
vival and early juvenile survival are linked to the  
female, as she chooses the spawning time and  
site, constructs the redd and deposits the nutri-  
ent-rich eggs. In Atlantic salmon, the survival of  
eggs in the nests not destroyed during incuba-  
tion (e.g., by scouring and nest superimposition,  
see below) may be as high as 74-91% until hatch-  
ing (Shearer 1961, MacKenzie and Moring 1988).  
When the eggs hatch, the small juveniles still  
have a considerable amount of nutrients and en-  
ergy stored in the yolk-sac as a result of maternal  
provisioning (Einum and Fleming 1999, Berg et  
al. in press). Once the yolk sac is absorbed, the  
juveniles emerge from the gravel into the open  
water. Loss rates during the first weeks thereaf-

ter are very high, with 68-88% mortality during the first 17-28 days (Einum and Fleming 2000a,b). Similar patterns have been observed in brown trout, where about 80% of fry rarely feed after emergence, quickly lose weight and drift downstream during night and die (Elliott 1986; see also Héland 1980a, b). Incubation and early juvenile life are thus periods of intense selection (Elliott 1994, Einum and Fleming 2000a,b).

**Spawning Time** – A female's spawning time will dictate the thermal regime her embryos experience during development and to a large extent, their hatching and emergence time from the gravel as fry (e.g., Crisp 1981, Jensen et al. 1991). Peak spawning times between the earliest and latest breeding populations of a salmonid species may range by several months (Groot and Margolis 1991, Fleming 1996). The timing among populations correlates with water temperature during incubation (Heggberget 1988), likely to ensure optimal timing of hatching and initial feeding for the offspring (Brannon 1987, Heggberget 1988, Quinn et al. 2000). Other factors such as water-flow regime during egg incubation or limited access to the breeding grounds due to river freeze-up might also be important (Fleming 1996).

Within populations, spawning may extend over many weeks (e.g., Fleming and Gross 1989, Tallman and Healey 1994, Fleming 1996, Blanchfield and Ridgway 1997), and may be temporally segregated between upper and lower reaches of the river, particularly in large systems where environmental conditions differ (Burger et al. 1985, Webb and McLay 1996). In addition to within-river variability in environmental conditions, intraspecific breeding competition may be an important factor affecting spawning times (Schroder 1981, Fleming and Gross 1993, Elliott 1994, Petersson and Järvi 1997). For the offspring, spawning time will affect emergence time, with early emerging fry having an advantage in establishing territories, and beginning to feed and grow before late emergers (Fausch and White 1986, Chandler and Bjornn 1988, Brännäs 1995). Metcalfe and Thorpe (1992) showed that Atlantic salmon emerging first were dominant, grew faster and smolted a year earlier than later emerging conspecifics. Moreover, Einum and Fleming

(2000a) identified directional selection for early emergence in Atlantic salmon due to differential survival and influences on body size. The advantages of early offspring emergence and ready access to highest-quality nest sites, however, must be traded off against susceptibility to nest destruction by digging activity of later-breeding females and probability of unfavourable environmental conditions early in the spring during emergence. These trade-offs may generate adaptive variation in spawning time within populations and result in the evolution of adaptive temporal variation in life history traits ("adaptation-by-time", Hendry et al. 1999).

**Spawning Site** – Female choice of spawning site will dictate the environment her embryos and subsequently, her emerging offspring will experience as fry. Poor quality nests, having high concentrations of fine sediment/sand and thus poor permeabilities and low intragravel dissolved oxygen will severely reduce embryo survival (reviewed in Chapman 1988). Location will also be critical to the emerging fry, which initially remain in the nest's vicinity due to their poor swimming ability and negative buoyancy. Thus, females unable to choose and/or fight for a good site will expose her offspring to potentially harsh environmental conditions and thus high mortality immediately after emergence. For example, proximity of the spawning site to suitable nursery habitat, particularly downstream (Elson 1962, Gibson 1993), may be important as fry slowly disperse. Egg burial depth will be important in decreasing the probability of egg destruction by scour during spates and by nest superimposition by later spawning females (e.g., Crisp 1989, van den Berghe and Gross 1989, Steen and Quinn 1999). While deeply buried embryos could suffer from inadequate water flow, evidence from chum salmon (*O. keta*) suggests this is not necessarily the case possibly because larger females, which dig deeper nests, do so in faster water than small females (Peterson and Quinn 1996). In general, egg burial depth increases with female size (reviewed in DeVries 1997), suggesting that it is selectively advantageous.

**Egg size** – How a female partitions her resources available for egg production has impor-

tant fitness consequences affecting the number of surviving offspring she can expect. Large eggs give rise to larger juveniles than smaller ones (e.g., Fowler 1972, Gall 1974, Pitman 1979, Thorpe et al. 1984), which in turn may afford faster juvenile growth (Bagenal 1969), higher status (Wankowski and Thorpe 1979), reduced susceptibility to starvation (Hutchings 1991), predation (Parker 1971) and parasites (Boyce 1974), or in other words, better offspring survival. However, large egg size appears to be at the cost of reduced egg number (fecundity) (Svärdson 1949, Fleming and Gross 1990, Quinn and Bloomberg 1992, Jonsson et al. 1996). Theory suggests that natural selection should maximise a female's fitness returns per unit of resource invested in egg production. This will be accomplished by dividing that investment into eggs of optimal size (Smith and Fretwell 1974, Parker and Begon 1986, Roff 1992). Thus, for a given amount of resources for egg production, egg number should vary in response to selection upon egg size. Einum and Fleming (2000b) tested this by manipulating egg size in Atlantic salmon and showed that the joint effect of egg size on egg number and offspring survival resulted in stabilising phenotypic selection for an optimal size. A size that closely matched the mean egg size in the population, but was below that that maximised offspring survival. The results indicated that egg size had evolved largely in response to selection on maternal rather than offspring fitness.

In another study, Einum and Fleming (1999) found distinct reaction norms in the performance of juvenile brown trout from small and large eggs, with growth and survival being similar in high quality environments but becoming increasingly divergent in poorer environments. The existence of such reaction norms indicates that the optimal egg size varies across gradients of environmental quality, and this has likely shaped the evolution of egg size. This may help explain why the eggs of individual females are fairly uniformed in salmonid fishes (Fleming and Ng 1987, Fleming et al. 1996), while among females and across population eggs may differ more than twofold in weight (Beacham and Murray 1993, Fleming 1998). Like fecundity, egg size typically increases with fe-

male size, such that larger females forgo more eggs to have larger eggs for their body size than do small females. This suggests that the optimal egg size likely varies in relation to abiotic and biotic factors as affected by female size. For example, because larger females deposit more eggs on average in their nests than smaller females (Fleming 1996), sibling competition at emergence is likely to be more intense and hence select for a larger optimal egg size (cf. Parker and Begon 1986). Alternatively, female size may influence the quality of incubation habitat her eggs experience (van den Berghe and Gross 1989; modelled by Hendry et al. in press). Small females, which are often less competitive than larger females, may be forced to use sub-optimal substrate, having high proportions of fine sediment, limited intra-gravel water movement and low levels of dissolved oxygen. Such sub-optimal incubation substrate may select against large eggs, because of their higher metabolic demands and less efficient surface-to-volume ratio for acquiring oxygen (van den Berghe and Gross 1989). Quinn et al. (1995) found a positive association between egg size and substrate size in sockeye salmon (*Oncorhynchus nerka*), suggesting adaptation in response to spawning site quality. Furthermore, under conditions of intense nest competition, some large females may also be displaced into poor nesting environments and thus incur lower success than smaller females (Holtby and Healey 1986), which over time should select for a smaller average egg size within the population.

## What is known about the reproductive patterns of released fish?

As evident from the previous discussion, the evolution and dynamics of the breeding system of salmonid fishes is complex, having important consequences for the demographic and genetic structure of populations. The release of hatchery fish will almost certainly affect this structure and understanding the reproductive patterns of the released fish will be important in predicting their effect on the population's natural productivity.

The reproductive traits of released fish will reflect the stock's genetic origin, rearing history (domestication effects) and form of rearing (environmental effects). The term 'domestication' has been applied differently, though all agree that it involves animals being 'farmed by' man in a human-imposed environment. This process inevitably results in evolutionary changes due to intentional and unintentional artificial selection by humans and random genetic effects (e.g., bottlenecks, founder effects). A conservative viewpoint holds that domestication should be defined as involving certain irreversible changes of the animal exposed to the new environment as a result of an active selection procedure by man (cf. Hemmer 1990). From this point of view, there are very few 'true' domestic fishes in the world, though the carp (*Cyprinus carpio*), which has been intentionally selected for over 2000 years (Ling 1977), would likely qualify. A more liberal viewpoint holds that domestication involves all forms of evolutionary change due to artificial rearing, not just those due to intentional selection. The use of the term 'domesticated' for hatchery-reared fish has a long history, and was, for example, used in the 1950's (see e.g., Wood et al. 1957). For practical reasons we concur with this traditional use of the term.

Most studies examining the reproductive traits of released fish have thus far been laboratory studies, in a broad sense; i.e. comparisons of the behaviour of wild and domesticated fish in controlled environments such as aquaria, stream channels or small enclosed areas of rivers. In addition, most studies have compared wild and multi-generation hatchery fish, often of differing genetic origins, thus making it difficult to separate genetic from environmental effects. This, however, is not surprising given the scale at which these experiments must be conducted, and the fact that for most hatchery stocks their founding wild population has been altered by large-scale introgression from hatchery fish. Nevertheless, in this section we will attempt to address the environmental and genetic (domestication and non-native origin) effects of hatchery rearing on the reproductive traits of released fish.

## Age and size at maturity

Typically, hatchery-rearing leads to rapid growth of fish due to *ad libitum* food availability, which can affect the age and size at maturity. Early (i.e. precocial) maturity among male salmonids is well known to be positively related to growth (e.g., Alm 1959, Saunders et al. 1982, Gross 1996). Thus, releases of parr that have experienced rapid growth in hatcheries may affect mating dynamics in wild populations by dramatically increasing the number of mature male parr. Rapid juvenile growth can also result in low age-at-smolting (e.g., Metcalfe et al. 1989, Økland et al. 1993) and subsequently, age-at-maturity. Moreover, the proportion of fish returning as grilse (one-sea-winter) is positively correlated with the size of smolts released (Chadwick 1988, Chadwick and Clayton 1990, Crozier and Kennedy 1993). A decrease in the age- and thus, size-at-maturity is a pattern observed in hatchery-supplemented populations of Atlantic salmon (e.g., Christensen and Larsson 1979, Sharov and Zubchenko 1993). In addition to environmental effects due to growth rate, there are indications that such responses may also reflect domestication selection in hatchery populations (Kallio-Nyberg and Koljonen 1997, also Fleming and Gross 1989). The effects of domestication on size-at-maturity, however, may not be straight forward as evidenced by the apparent lack of effect on Atlantic salmon and positive effect on brown trout of the Älvkarleby hatchery, Sweden (Pettersson et al. 1996).

## Homing

Generally, the homing precision of returning hatchery adults released as freshwater juveniles or as smolts in rivers is much higher than that for fish escaping or being released at marine sites, without any connection with a river (Hansen and Jonsson 1994, Hansen and Quinn 1998). Smolts and post-smolts escaping or released from a marine site return to the area in the sea from which they escaped/were released, but because of a lack of home-river imprinting, the sexually mature fish will enter several rivers in that area to spawn late in the season (Sutterlin et al. 1982, Gunnerød et

al. 1988, Hansen et al. 1989). For example, experiments in the Baltic in the early 1980s demonstrated that transporting smolts to sea pens and delaying their release a few months dramatically improved survival, however, it also significantly increased their rate of straying (Anon. 1997). Similarly, hatchery Atlantic salmon released as smolts at a river mouth return there as adults at a similar time as wild fish, but ascend the river later apparently due to a lack of juvenile experience with the river (Jonsson et al. 1990, 1991; cf. McKinnell et al. 1994, Petersson and Järvi 1993). Also, the timing of release of smolts and post-smolts can affect straying, with those released during winter straying more and farther away than fish released during the rest of the year (Hansen and Jonsson 1991). As a rule of thumb, fish released at the wrong time and at the wrong site stray more, i.e. have worse homing behaviour, than those released at more appropriate (natural) times and sites (reviewed by Quinn 1993).

### Spawning time and location

If hatchery fish differ from wild fish in location or timing of spawning the implications for offspring survival can be critical (see above). In a study of coho salmon (*O. kisutch*) in Oregon, Nickelson et al. (1986) found that hatchery fish returned and spawned earlier than the native wild fish, and concluded that this was largely responsible for the failure to rebuild populations in streams stocked with presmolt hatchery fish. Spawning time has a high heritability in salmonid fishes (Siitonen and Gall 1989, Silverstein 1993, Gharrett and Smoker 1993, Quinn et al. 2000) and evidence suggests that unintentional hatchery selection for early spawners can alter it (Ayerst 1977, Leider et al. 1984, Flagg et al. 1995, Petersson and Järvi 1993). There are also indications that hatchery rearing can affect the choice of spawning location. Not only do fish having experienced only the lower reaches of the river (as normally is the case for released hatchery-reared fish) hesitate to ascend to the upper parts where the spawning grounds lie, they also wander more within the river than wild fish (Jonsson et al. 1990, 1994). An interesting potential outcome of altered

choice of spawning time and location is increased interspecific hybridisation due to a breakdown of spatial and/or temporal isolation between species (Leary et al. 1995, Jansson and Öst 1997).

### Fecundity and egg size

The relaxation (or perhaps even removal) of sexual and natural selection, and the artificial nature of the hatchery breeding process will likely favour those individuals that allocate their available resources to gonads instead of elaborate secondary characteristics or energy-demanding spawning activities (Fleming and Gross 1989). However, the few studies that have tested this hypothesis have been indirect (i.e. comparative or time series analyses; Table 1). To examine whether a general pattern exists among these studies we used a meta-analytical approach. Such an analysis combines the separate significance tests from the different data sets that test the same scientific (but not statistical) hypothesis. Each independent test reports a probability value for the particular outcome, assuming the null hypothesis to be correct. From the studies listed in the Table 1, we extracted probability values relevant for the trait concerned (i.e. total egg biomass). These probability values were combined according to Sokal and Rohlf (1995) to create an overall test of significance. The meta-analysis identified weak support, at best, for increased gonad allocation with hatchery rearing ( $\chi^2 = 20.81$ ,  $df = 12$ ,  $P = 0.054$ ). Such effects may be small and masked by other trade-offs and factors, such as body condition, and thus carefully designed investigations may be needed to reveal differences.

There are indications that hatchery-rearing may affect female allocation (size-adjusted) to egg size (6 of 8 studies, Table 1), however, the pattern appears inconsistent (meta-analysis:  $\chi^2 = 13.78$ ,  $df = 16$ ,  $P = 0.62$ ). Fleming and Gross (1990) hypothesized that the elimination of the constraint of gravel quality that eggs experience in nature (van den Berghe and Gross 1989, Quinn et al. 1995) will favour larger eggs in hatcheries because of survival and growth advantages. In addition, if incubation temperatures in hatcheries are higher than in nature this may also select for

Table 1. Differences in egg production traits between wild and hatchery populations of salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

| Trait             | Effect        | Origin of Effect | Origin of Hatchery Fish | Length of Propagation | Species         | Reference                |
|-------------------|---------------|------------------|-------------------------|-----------------------|-----------------|--------------------------|
| Total Egg Biomass | Increase*     | G + E            | Native                  | 4-83 years            | Coho salmon     | Fleming and Gross 1989   |
|                   | Increase      | G + E            | Non-native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                   | Not different | G + E            | Native                  | 25+ years             | Brown trout     | Petersson and Järvi 1993 |
|                   | Not different | G > E            | Native                  | 25 years              | Atlantic salmon | Petersson et al. 1996    |
|                   | Not different | G > E            | Native                  | 25 years              | Brown trout     | Petersson et al. 1996    |
|                   | Not different | E                | Native                  | First generation      | Atlantic salmon | Jonsson et al. 1996      |
| Egg Size          | Increase      | G + E            | Native                  | 4-83 years            | Coho salmon     | Fleming and Gross 1990   |
|                   | Increase      | G + E            | Non-native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                   | Not different | G + E            | Native                  | 4-83 years            | Coho salmon     | Beacham and Murray 1993  |
|                   | Not different | G + E            | Native                  | 25+ years             | Brown trout     | Petersson and Järvi 1993 |
|                   | Increase      | G > E            | Native                  | 25 years              | Brown trout     | Petersson et al. 1996    |
|                   | Increase      | G > E            | Native                  | 25 years              | Atlantic salmon | Petersson et al. 1996    |
|                   | Decrease      | E                | Native                  | First generation      | Atlantic salmon | Jonsson et al. 1996      |
|                   | Decrease      | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |

\* Not significant at  $P = 0.082$

larger eggs because of reduced efficiency of conversion of yolk to body tissue (Heming 1982) and increased maintenance costs associated with increased water temperature (Hamor and Garside 1977). Thus, hatchery populations exposed to selection over generations may be expected to show increased egg sizes. Support for this, however, has been inconclusive and based on comparative and time-series analyses that do not fully control for other potential factors (e.g., gene flow, environment, phylogeny; Fleming and Gross 1990, Petersson et al. 1996; Beacham and Murray 1993, Petersson and Järvi 1993). By contrast, more controlled studies examining single generation (environmental) effects of hatchery rearing indicate a decrease in egg size (Jonsson et al. 1996, Fleming et al. 1997). It has been proposed on theoretical grounds that egg size should be sensitive to juvenile growth and survival (Sibly and Calow 1986, Winemiller and Rose 1993), and its expression phenotypically plastic in spatially and temporally varying environments (Perrin 1988). This appears to be the case among at least some salmonids, where egg size is negatively associated with early maternal growth (Thorpe et al. 1984, Jonsson et al. 1996, Morita et al. 1999, Tamate and Maekawa 2000). Such a phenotypically plastic response may also over time select for reduced egg size, if competition among newly emerged fry is reduced relative to that experienced in nature. While there are clear indications that hatchery rearing affects egg size, the direction of response, particularly the long-term evolutionary response remains less clear. The important point here, however, is that any alteration in egg size is likely to have important implications for the success of hatchery releases (cf. Einum and Fleming 2000b).

### Breeding morphology

Morphology affects an individual's performance, and thereby its fitness (Arnold 1983). Fish morphology is under conflicting selection pressures (e.g. Riddell and Leggett 1981, Fleming and Gross 1989, Swain and Holtby 1989), and there are clear relationships between form and function (Robinson and Wilson 1996), so that body shape af-

fects swimming performance (e.g., Skúlason et al. 1989). The hatchery environment exposes the fish to new developmental and evolutionary forces that may not only effect juvenile (reviewed in Einum and Fleming 2001), but also adult phenotypes. Hatchery adults appear to show reduced expressions of morphological characters important during breeding, such as secondary sexual characters (Fleming and Gross 1989, 1994, Petersson and Järvi 1993, Hard et al. 2000). Both environmental and genetic (domestication) factors appear responsible for these changes (Fleming et al. 1994). Such reduced expressions of secondary sexual characters can have negative consequences for natural breeding success (see below).

### Breeding behaviour

Like morphology, the breeding behaviour of hatchery fish is predicted to be influenced by environmental effects and the relaxation, removal and/or alteration of natural and sexual selection. Experimental studies under semi-natural conditions indicate that these effects become evident primarily when hatchery fish breed sympatrically with, and face competition from wild fish (Fleming and Gross 1992, 1993, Fleming et al. 1996, 1997, Berejikian et al. 1997, Petersson and Järvi 1997). For hatchery females in competition with wild females, indicators of inferior competitive ability include delays in the onset of breeding (Fleming and Gross 1993), fewer nests (meta-analysis:  $\chi^2 = 24.66$ ,  $df = 10$ ,  $P = 0.006$ , Table 2) and greater retention of unspawned eggs (Fleming and Gross 1993, Fleming et al. 1996). This often occurs despite similar levels of overt aggression by hatchery and wild females ( $\chi^2 = 5.64$ ,  $df = 12$ ,  $P = 0.93$ , Table 2; but see Petersson and Järvi 1997). Hatchery females also appear more likely to have their eggs fertilised by several secondary males (most likely parr) than wild females, suggesting either poorer defence against, and/or a greater willingness to have secondary males present (Thompson et al. 1999). Ultimately, the breeding success of hatchery fish is frequently inferior to that of wild females ( $\chi^2 = 19.97$ ,  $df = 6$ ,  $P = 0.003$ , Table 2).

The breeding behaviour of males appears more

strongly affected by hatchery rearing than that of females, reflecting the greater intensity of selection on male competitive ability during this period. Hatchery males tend to be less aggressive (meta-analysis:  $\chi^2=24.54$ ,  $df=12$ ,  $P=0.017$ ) and less active courting females (meta-analysis:  $\chi^2=60.38$ ,  $df=12$ ,  $P<0.001$ ), and ultimately achieve fewer spawnings than wild males (meta-analysis:  $\chi^2=48.59$ ,  $df=10$ ,  $P<0.001$ ; Table 1). Across the studies reported in Tables 2 and 3, hatchery males suffer more from inferior breeding performance than hatchery females. This pattern also appears to carry over into the wild, where gene flow between cultured and wild salmonids is sex biased, principally involving wild males mating with cultured females (Fleming et al. 2000). The presence of male parr of cultured origin, however, could change this substantially (Fleming, unpublished data).

In most studies, environmental and genetic factors affecting the breeding behaviour of hatchery fish cannot be definitively separated. Fleming et al. (1997) in a study controlling for the genetic background of the fish, however, revealed that the environmental effects of hatchery-rearing up to smolting could be significant. They found differences in the breeding performance of hatchery and wild male, but not female Atlantic salmon. While having similar levels of aggression, hatchery males were involved in more prolonged aggressive encounters and incurred greater wounding and mortality than wild males. Furthermore, hatchery males were less able to monopolise spawnings and obtained an estimated 51% the breeding success of wild males. In another study, Fleming and Gross (1994) were able to experimentally quantify the intensity of natural and sexual selection on different male and female morphological traits, as well as behavioural differences between multi-generation hatchery and wild coho salmon. They revealed direct (i.e. independent) selection on body size, the secondary sexual trait hooked snout (significantly larger in wild than hatchery males), and hatchery-wild behavioural differences associated with breeding success. Such information provides a basis for predictions about effects of relaxed or altered selective pressures in hatcheries.

## Breeding success and the contribution to natural productivity

Clearly, an array of changes in behavioural, life history and morphological traits associated with reproduction occur in culture environments and these may have important implications for the ability of released fish to contribute to natural productivity. The success of release programs must lie in their ability to allow fish to bypass the high mortality of early life in the wild (see above) and then to survive, breed and produce offspring that *contribute* to natural production in the wild (Waples et al. in press). The word “contribute” is important here, for it means that the released fish should not take away from the production of the wild population, if it still exists. Our aim in this section thus is to review the literature for evidence regarding the contribution of released salmonids to natural productivity.

The best examples of successful contribution come from the release of salmonids to re-establish extirpated populations (i.e. driven to extinction) once the cause(s) of extinction have been remedied or to introduce fish into areas formerly inaccessible to natural colonisation due to an obvious physical barrier (Ricker 1972, Withler 1982). Success appears to reflect the presence of an open or unsaturated niche, i.e. the absence of competition from local con- and/or heterospecifics. Such programs should be short term, aiming to establish populations rapidly and then once founded, allow natural selection to shape the population to its local environment. Continued releases are only likely to hindered proper establishment, i.e. adaptation to local conditions. This may be particularly problematic if the habitat has been altered in ways that require the fish to re-adapt (e.g., following hydropower development). What is unclear about such releases is whether they are any better in the long term than natural colonisation through straying from nearby populations, if the possibility exists. This, however, has never been addressed and unfortunately in our current environment, may be nearly impossible to examine because the vast

Table 2. Female reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

| Trait            | Effect        | Origin of Effect | Origin of Hatchery Fish | Length of Propagation | Species         | Reference                |
|------------------|---------------|------------------|-------------------------|-----------------------|-----------------|--------------------------|
| Overt Aggression | Not different | G + E            | Non-Native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                  | Not different | G + E            | Non-Native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                  | Not different | G + E            | Non-Native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                  | Not different | E > G            | Non-Native*             | First generation      | Coho salmon     | Berejikian et al. 1997   |
|                  | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
|                  | Less          | G + E            | Native                  | 26-27 years           | Brown Trout     | Petersson and Järvi 1997 |
| Number of Nests  | Not different | G + E            | Non-native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                  | Not different | G + E            | Non-native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                  | Fewer         | G + E            | Non-native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                  | Fewer         | E > G            | Non-Native*             | First generation      | Coho salmon     | Berejikian et al. 1997   |
|                  | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
| Breeding Success | Lower         | G + E            | Non-native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                  | Lower         | G + E            | Non-native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                  | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
|                  | Lower         | G + E            | Non-native*             | 23 years              | Atlantic salmon | Fleming et al. 2000      |

\* Fish were captively reared to maturity

Table 3. Male reproductive behaviour of hatchery relative to wild salmonids. Effect: whether the trait expression in the hatchery fish differs from that in wild fish and in what direction. Origin of Effect: G + E = genetic and environmental, E = predominantly environmental, G = predominantly genetic, G > E = genetic effects suspected to be greater, E > G = environmental effects suspected to be greater.

| Trait               | Effect        | Origin of Effect | Origin of Hatchery Fish | Length of Propagation | Species         | Reference                |
|---------------------|---------------|------------------|-------------------------|-----------------------|-----------------|--------------------------|
| Overt Aggression    | Less          | G + E            | Non-native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                     | Less          | G + E            | Non-native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                     | Less          | G + E            | Non-native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                     | Not different | E > G            | Non-native*             | First generation      | Coho salmon     | Berejikian et al. 1997   |
|                     | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
|                     | Not different | G + E            | Native                  | 26-27 years           | Brown trout     | Petersson and Järvi 1997 |
| Courting            | Less          | G + E            | Non-native              | 15 years              | Coho salmon     | Fleming and Gross 1992   |
|                     | Less          | G + E            | Non-native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                     | Less          | G + E            | Non-native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                     | Less          | E > G            | Non-native*             | First generation      | Coho salmon     | Berejikian et al. 1997   |
|                     | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
|                     | Less          | G + E            | Native                  | 26-27 years           | Brown Trout     | Petersson and Järvi 1997 |
| Number of Spawnings | Fewer         | G + E            | Non-native              | 15-16 years           | Coho salmon     | Fleming and Gross 1993   |
|                     | Fewer         | G + E            | Non-native*             | 20 years              | Atlantic salmon | Fleming et al. 1996      |
|                     | Fewer         | E > G            | Non-native*             | First generation      | Coho salmon     | Berejikian et al. 1997   |
|                     | Not different | E                | Native                  | First generation      | Atlantic salmon | Fleming et al. 1997      |
|                     | Fewer         | G + E            | Native                  | 26-27 years           | Brown Trout     | Petersson and Järvi 1997 |
|                     |               |                  |                         |                       |                 |                          |

\* Fish were captively reared to maturity

majority of strays are domesticated fish (farm escapees and hatchery strays).

Other examples of successful contributions from released salmonids are rare, if not non-existent. The most common form of release program is aimed at the supplementation of wild populations, i.e. the intentional integration of hatchery and natural production, with the goal of improving the status of an existing natural population (Finstad et al. 2000, Fjellheim and Johnsen 2001, Vøllestad and Hesthagen 2001, Waples et al. in press). Such integration, however, entails significant ecological and genetic risks to the wild population (e.g., Hindar et al. 1991, Waples 1991, Youngson and Verspoor 1998, Einum and Fleming 2001), as well as potential benefits. Yet, despite the vast majority of release programs involving supplementation and its importance as a management strategy, astonishingly little has been done in Norway and other countries to evaluate its effectiveness to meet its principal objective/goal.

The evidence that does exist is generally qualitative and indirect, based on genetic studies of introgression and ecological studies of correlates of breeding success or semi-natural experiments (Table 4). While genetic studies often provide quantitative estimates of introgression, they provide little information regarding the actual relative contribution of the released to wild fish to the natural production. For example, frequently the levels of introgression observed are the result of large-scale releases over many years. By this process, introgression must almost be inevitable. However, what is striking from our somewhat limited review of the literature is that 45% (14 of 31) of the investigations reported little or no evidence of introgression (Table 4). Thus, despite large-scale releases in many of these cases, the supplementation programs must be deemed failures. In *none* of the studies reporting significant introgression, is there information on whether the release program resulted in improved natural production of the population. Moreover, these genetic studies provide little clue as to the underlying determinants of introgression (e.g., relative lifetime reproductive success) or lack thereof. At a broad scale, however, Utter (2000)

noted a pattern of greater resistance to introgression among anadromous than among comparable freshwater populations, suggesting that more complex adaptations associated with an anadromous life history may be responsible (cf. Hansen et al. 2000).

All the ecological evidence points to diminished lifetime reproductive success and abilities of hatchery-released salmonids to contribute to natural productivity (Table 4). These studies identify critical life history episodes, particularly breeding, juvenile emergence and first year life, as key determinants of introgression (see also McGinnity et al. 1997, Fleming et al. 2000, review by Einum and Fleming, 2001). They also identify not only the directions of gene flow, but more importantly the causes for sex biases and general predictive models as to when and how such biases arise. Quantitative experimental evidence indicates that among anadromous adults, gene flow into wild populations occurs mainly via hatchery females because of the intense competition that hatchery males face from wild males (Fleming and Gross 1993, Fleming et al. 1996, 1997, 2000). However, where males have the opportunity to mature early as parr or as resident fish, such males may make significant genetic contributions to the population (Hansen et al. 2000). This likely results from their large size at release, which can influence both the propensity to mature early (e.g., Alm 1959, Thorpe 1986) and competitive ability (Jones 1959, Thomaz et al. 1997) relative to that of wild fish. The most complete evidence on relative lifetime reproductive performance of hatchery fish comes from two natural experiments that suggest that released fish have approximately a tenth the ability of wild fish to contribute to natural productivity (Table 4; see also Fleming et al. 2000). Neither study, however, examined whether the contribution of the released fish actually added to, or simply replaced the natural productivity of the wild fish. Addressing this latter issue is extremely important, but difficult, requiring an experimental design that incorporates manipulations (i.e. adding hatchery fish) and controls (i.e. excluding hatchery fish) on both spatial and temporal scales. Such experiments are expensive, long term and require man-

agement vision to address this vitally important question on the contribution of released fish to natural productivity.

In probably the most thorough attempt to date to examine the ability of supplementation programs to contribute to natural productivity, Waples et al. (in press) reviewed 19 such programs developed for Pacific salmon. Of those, nine populations showed an increase or had remained stable in size since the start of supplementation, while the remainder (10) had declined. They also found that supplemented and unsupplemented (control) populations showed similar trends in four of the six possible comparisons, while the supplemented population outperformed the control in one case and the reverse occurred in the other. Moreover, for two programs it was possible to compare the populations' status before and after supplementation had ended, and both remained "at risk". It thus seems clear that the supplementation of depressed natural populations using hatchery fish seldom achieves the objective of increased natural production (cf. Steward and Bjorn 1990). Predicting the outcome of a release must be considered a highly complex, and as yet unresolved problem, involving ecological and genetic factors.

## Conclusions

The current review indicates that understanding breeding dynamics and reproductive success are critical to predicting effects of various conservation and supplementation programs, through their effects on the demographically and genetically effective population size, and gene flow. The value of reproductive performance in hatchery fish depends on the management goal. If the goal is to re-establish or rebuild wild populations for conservation purposes (i.e. conservation releases), current hatchery practices appear to result in competitively and reproductively inferior fish that limit their effectiveness. Long-term application of such releases will moreover inhibit local adaptation and thus natural productivity. On the other hand, if the goal is to supplement wild populations to increase fisheries (i.e. fisheries releases) while reducing impacts on the wild popula-

tions, such reproductive inferiority could be advantageous, limiting the negative effects of introgression. However, the threats of ecological interference and altered selection regimes associated with the introduction of hatchery fish remain. Moreover, reproductive isolation is likely to remain incomplete and even limited introgressive hybridisation may pose a concern, particularly when the scale of hatchery introductions is significantly greater than that of natural production. Clearly, the appropriate and effective use of hatcheries will be a balancing act.

Poorly managed hatchery programs can alter or even destroy biological diversity of species/populations. This does not mean, however, that we should give up on the hatchery concept as a management tool, particularly for populations facing high short-term risk of extinction. Rather, hatcheries need to be modified to minimise the detrimental effects of hatchery rearing on fish phenotypes and genotypes, including morphological and behavioural traits, and thus increase the potential for successful enhancement. We must also recognise an inherent conflict that exists in the way hatcheries currently function, to both conserve threatened wild populations and to enhance fisheries (cf. Fleming 1994). The use of hatcheries for the enhancement of fisheries will often directly threaten the existence of wild populations, particularly those in need of conservation, through direct and indirect genetic effects (reviewed by Hindar et al. 1991, Waples 1991). Finally, we must recognise that release programs are not a solution to conservation problems, but rather should be thought of as a short-term aid for wild populations at risk. Conservation will only be successful if causes of decline in wild populations are remedied.

The biggest gap in our knowledge is understanding the performance of hatchery-produced fish and their progeny in the natural environment. Can release programs, particularly those designed for conservation, provide a net long-term benefit to natural populations? Moreover, when do we implement such programs, and then how do we best manage them to achieve this? Ideally, evaluations of supplementation programs should be conducted over a number of generations to

Table 4. Evidence of the ability of salmonid supplementation programs to contribute to the natural productivity of populations.

| Type of Evidence  | Frequency of release  | Origin of Hatchery fish      | Life stage at release      | Species         |
|---|---|------------------------------|----------------------------|-----------------|
| <i>Significant Interbreeding/Contribution to Natural Productivity</i> |   |                              |                            |                 |
| Genetic   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1968-83)  | Non-local                    | Eyed eggs, 0+ fry, 1+ parr | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (6-20 years)   | Non-local                    | 0+ fry, adults             | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (20+ years)  | Non-local                    | 0+ fry                     | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1944-74)  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1970-92)  | Non-local                    | Eggs, fry                  | Brown trout     |
|   | Repeated (test over 2 years)  | Non-local                    | —                          | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1980-1992)  | Non-local                    | 0-2+, smolts               | Brown trout     |
|   | Repeated  | Non-local                    | Primarily smolts           | Chinook salmon  |
|   | Repeated  | Non-local                    | —                          | Cutthroat trout |
|   | Repeated  | Non-local                    | —                          | Rainbow trout   |
|   | Repeated (1938-95)  | Non-local                    | Fingerlings, yearlings     | Rainbow trout   |
|   | <i>Strongly Diminished or No Interbreeding/Contribution to Natural Productivity</i> |                              |                            |                 |
| Experimental  | Single (1989)   | Non-local                    | Adults                     | Brown trout     |
|   | Repeated (1976-79)  | Non-local, but same drainage | Smolts                     | Steelhead trout |
| Genetic   | Repeated (1950-76)  | Non-local                    | Fry                        | Atlantic salmon |
|   | Single (1990)   | Non-local                    | 0+ parr                    | Atlantic salmon |
|   | Repeated (6-20 years)   | Non-local                    | 0+ fry, adults             | Brown trout     |
|   | Repeated (20 years)   | Non-local                    | 0+                         | Brown trout     |
|   | Repeated  | Non-local                    | 0-2+                       | Brown trout     |
|   | Repeated (20+ years)  | Non-local                    | 0+ fry                     | Brown trout     |
|   | Repeated (1980-1992)  | Non-local                    | 0-2+, smolts               | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1966-89)  | Non-local                    | Eyed eggs, 0+, adults      | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Brown trout     |
|   | Repeated (1980-90's)  | Non-local                    | 0-2+, smolts               | Brown trout     |
|   | Repeated  | Non-local                    | —                          | Chinook salmon  |
|   | Repeated (1, 2, 4 years)  | Non-local                    | Eyed eggs                  | Chum salmon     |

Table 4. cont.

| Observation  | Reference   |
|--|---|
| <i>Significant Interbreeding/Contribution to Natural Productivity</i>  |   |
| Genetic admixture of native and hatchery fish (Sweden)   | Ryman 1981  |
| Natural-spawning hatchery fish 42% genetic contribution to 0+ juveniles; excessive heterozygosity (N. Ireland)   | Taggart and Ferguson 1986                                     |
| Introgression common (France)  | Barbat-Leterrier et al. 1989                                  |
| Introgression rates up to 80% in some areas (France)   | Guyomard 1989   |
| Replacement of 2 natural river populations and near elimination of another (Spain)   | Garcia-Marin et al. 1991                                      |
| Strong introgression in 2 lake populations (Spain)   | Martínez et al. 1993  |
| Introgression rates of ca. 75% (Greece)  | Apostolidis et al. 1996, 1997                                 |
| Introgression rates of 30-70% at 4 of 6 stocked localities (Italy)   | Giuffra et al. 1996   |
| Natural breeding and some introgression, but positive assortative mating common (Switzerland)  | Largiadè and Scholl 1996                                      |
| 2-55% introgression (Spain)  | Cagigas et al. 1999   |
| 10% introgression within 2 years (Spain)   | Garcia-Marin et al. 1999                                      |
| Introgression as high as 77% (France)  | Berberi et al. 2000   |
| Up to 46% introgression with resident fish (Denmark)   | Hansen et al. 2000  |
| Genetic homogenisation in areas of intense hatchery culture (USA Pacific Northwest)  | Utter et al. 1989   |
| Extensive introgression between subspecies in the (USA Pacific Northwest)  | Gyllensten et al. 1985  |
| 5 of 8 populations are interior-coastal hybrid swarms (Western USA)  | Williams et al. 1996  |
| Lower river pure, upper river a hybrid swarm (Oregon, USA)   | Williams et al. 1997  |
| <i>Strongly Diminished or No Interbreeding/Contribution to Natural Productivity</i>  |   |
| Despite more hatchery than wild spawners, only 16-19% genetic contribution to 0+ juveniles; survival 3 times lower for hatchery-wild hybrids than wild fish to age 2+ (Norway) | Skaala et al. 1996  |
| Success from breeding to 0+ juveniles 75-79% that of wild fish; lifetime reproductive success 11-13% that of wild fish (WA, USA)   | Chilcote et al. 1986, Leider et al. 1990, Campton et al. 1991 |
| Despite large releases of anadromous fish, landlocked salmon not detectably altered (Norway)   | Vuorinen and Berg 1989  |
| No indication of genetic contribution among adult fish (Spain)   | Moran et al. 1994   |
| Introgression rates as low as 0% in some areas (France)  | Guyomard 1989   |
| No evident genetic contribution (Spain)  | Moran et al. 1991   |
| Intensive stocking with little or no evidence of genetic contribution (Denmark)  | Hansen et al. 1993, Hansen and Loeschcke 1994                 |
| No detectable genetic influence in several rivers (Spain)  | Martínez et al. 1993  |
| Introgression low among anadromous fish (Denmark)  | Hansen et al. 1995, 2000                                      |
| Introgression rates of < 10% in 2 of 6 stocked localities (Italy)  | Giuffra et al. 1996   |
| Reproduced and interbred, but contribution diminished over time (France)   | Poteaux et al. 1998   |
| Extensive stocking had limited genetic impact (Spain)  | Garcia-Marin et al. 1999                                      |
| Little or no introgression (Denmark)   | Hansen et al., in press                                       |
| No evidence that strays had homogenised genetic characteristics of wild population (Snake R., USA)   | Marshall et al. 2000  |
| Despite millions of released fish, genetic contribution small and disappearing (Russia)  | Altukhov and Salmenkhova 1987, 1990                           |

Table 4. cont.

| Type of Evidence  | Frequency of release | Origin of Hatchery fish | Life stage at release | Species         |
|---|----------------------|-------------------------|-----------------------|-----------------|
| <i>Strongly Diminished or No Interbreeding/Contribution to Natural Productivity</i> |                      |                         |                       |                 |
| Genetic   | Repeated             | Non-local               | —                     | Rainbow trout   |
| Ecological (Indirect)   | Repeated (1982-88)   | Local                   | Smolts                | Atlantic salmon |
|   | Single               | Local                   | Smolts                | Atlantic salmon |
|   | Repeated (1991-93)   | Local                   | Smolts                | Brown trout     |
|   | Repeated (1980-82)   | Non-local               | Pre-smolts            | Coho salmon     |
|   | Repeated (1988-89)   | Non-local               | Smolts                | Coho salmon     |
|   | Repeated (decades)   | Non-local               | Smolts                | Steelhead trout |

permit distinguishing ecological and genetic effects of fish culture, and to evaluate the effectiveness of natural selection to restore fitness in natural populations of mixed hatchery-wild ancestry (cf. Waples et al. in press). Releases of hatchery fish can be a valuable management tool in our attempts to conserve wild salmon populations, yet considerable risks exist.

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Table 4. cont.

| Observation  | Reference   |
|--|---|
| <i>Strongly Diminished or No Interbreeding/Contribution to Natural Productivity</i>  |   |
| No detectable introgression (ID, USA)  | Wishard et al. 1984   |
| 14% of females and 37% of males appeared not to have spawned (Norway)  | Jonsson et al. 1990   |
| Females similar, and males 51% the breeding success of wild fish (Norway)  | Fleming et al. 1997   |
| Males lower mating success (Sweden)  | Pettersson and Järvi 1999   |
| Densities of juvenile offspring lower in stocked than unstocked streams (OR, USA)  | Nickelson et al. 1986   |
| Males 62% and females 82% the breeding success of wild fish (BC, Canada)   | Fleming and Gross 1993  |
| Population productivity and proportion of hatchery fish among natural spawners negatively related (OR, USA)  | Chilcote 1997 cited in Waples 1999  |
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