

Implications of Stocking: Ecological Interactions Between Wild and Released Salmonids

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Abstract

The common management practice of introducing artificially produced fish into wild populations has raised concerns among fishery biologists. In part, these concerns arise from the observation that hatchery-produced fish commonly differ from wild fish in ways that may influence ecological interactions between them. In this review, we use a meta-analytical approach to provide quantitative tests for such differences and show that the hatchery rearing of salmonids results in increased pre-adult aggression, decreased response to predators, and decreased survival. Changes in growth rates are common, but less consistent. Changes in other fitness-related traits such as migration, feeding, habitat use and morphology also occur. Based on the presented evidence we conclude that differences between hatchery-reared and wild fish may have negative implications for the success of stocking programs. A number of studies reporting population responses to stocking support this, suggesting that the performance of hatchery fish and their interactions with wild fish is of such a character that many of the current stocking practices may be detrimental to the recipient population.

Keywords: hatchery releases, competition, predation, survival, growth.

Introduction

Deliberate releases of artificially produced fish into wild populations have recently caused concern among fishery biologists (e.g. Hindar et al. 1991, Saunders 1991, Waples 1991, Thomas and Mathisen 1993, Ryman et al. 1995, Youngson and Verspoor 1998). Although such releases are often implemented to compensate for reduced production caused by human induced habitat degradation, a range of potential ecological problems may be associated with this practice. First, stocking of large numbers of fish into a limited habitat will inevitably affect population density, at least initially. Thus, any density-dependent characteristics of the environment or of the fish

itself are potentially affected (cf. Elliott 1989, 1990). This numerical effect of stocking could, for example, include changes in the frequency of competitive interactions, levels of food availability, or a functional response of predators, and hence influence growth and survival of the wild fish. Theoretical considerations suggest that this may cause hatchery releases to increase temporal variability of population strength (Fagen and Smoker 1989). Second, hatchery fish may differ genetically and/or phenotypically from wild fish. Such differences may affect how stocked and wild fish interact, and thus cause effects of stocking beyond those due to pure density-dependence.

Here we review the literature dealing with such effects in salmonids, summarising what is known

about differences between hatchery- and wild-reared fish, and the implications these differences have for ecological interactions between the two types of fish. Literature data are used to examine whether the predicted effects of differences between the two types of fish have been observed in the wild. We also identify areas where research is needed to increase our knowledge about ecological interactions between hatchery and wild fish, and to establish better management practices.

Why do hatchery and wild fish differ?

Fish reared in hatchery facilities may differ from their wild conspecifics for three reasons. First, fish are highly phenotypically plastic and therefore their phenotypes may be shaped considerably by the rearing environment (e.g. Wootton 1994, Pakkasmaa 2000). The traditional way of rearing fish in hatcheries (i.e. high densities in flow-through tanks) shows little or no resemblance to natural rearing. In fact, most environmental characteristics that may influence fish development differ. This includes feeding regimes, density, substrate, exposure to predators, and interactions with conspecifics. It is not surprising that such differences can have substantial impacts on the resulting fish phenotype.

The second reason why hatchery fish may differ from wild fish is that the intensity and direction of selection differs between the two environments. Perhaps most importantly, survival during egg and juvenile stages is substantially higher in the hatchery environment than in the wild (reviewed by Jonsson and Fleming 1993). This means that genotypes that potentially are eradicated in the wild, by predation or starvation, are artificially brought through the vulnerable period of selection during early juvenile stages (Elliott 1989, Einum and Fleming 2000a, b). In theory, hatchery fish could also experience altered selection pressures. For example, the high juvenile density and abundance of food may select for behavioural and physiological traits that are disadvantageous in nature. The importance

of such altered selection is unknown, but the intensity of selection may be limited due to the low levels of mortality. However, this may not necessarily be so, if traits such as body size attained in the hatchery are tightly linked to survival after release, a period of intense mortality among hatchery fish. Such genetic changes due to relaxed and/or altered selection are likely to accumulate in stocks being cultured over multiple generations (e.g., when brood stock is consistently chosen from adults originating from hatchery produced smolts). Multi-generation hatchery stocks are thus likely to differ more from wild fish than first generation stocks where most of the changes are likely to be of environmental origin.

The third reason why hatchery fish may differ from wild fish is the use of non-native fish for stocking. Such procedures may introduce novel, genetically based characters into the wild population and break up co-adapted gene complexes that may lead to outbreeding depression (e.g. Gharrett and Smoker 1991). Fortunately, the potential importance of local adaptations is being increasingly acknowledged (reviewed by Ricker 1972, Taylor 1991), and the practice of releasing non-native fish has therefore decreased in frequency.

Intentional artificial selection may also generate genetic change in hatchery populations, as has occurred with commercially farmed fish (Einum and Fleming 1997, Fleming and Einum 1997). However, such selection is rarely performed in any systematic way in non-commercial hatcheries. Thus, studies reporting differences caused by such selection have been omitted in this review.

Studies of differences between hatchery and wild fish take three forms. (1) The most common form simply documents the existence of differences and speculates about their origins. More detailed studies attempt to identify (2) the environmental and/or (3) genetic origins of the differences. The first form of study usually compares fish hatched and reared in the hatchery with fish from the wild, and while the differences observed likely have an environmental component, additional effects due to genetic differences may ex-

Table 1. Differences in pre-adult aggression and response to predators between wild and hatchery populations of salmonids. Pos = hatchery population more aggressive, Neg = hatchery population less aggressive/ lower response to predators, 0 = no significant difference. E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental.

Trait	Origin of effect	Form of effect	Fish	Species	Reference
Aggression	E	Pos	Native	Coho salmon	Rhodes and Quinn 1998
	E > G	Pos	Non-native	Atlantic salmon	Fenderson et al. 1968 ¹
	E > G	Pos	Non-native	Cutthroat trout	Mesa 1991
	G	Neg	Non-native	Atlantic salmon	Norman 1987
	G	Pos	Non-native	Brook trout	Moyle 1969 ²
	G	0	Native	Brown trout	Johnsson et al. 1996 ³
	G	Pos	Non-native	Coho salmon	Swain and Riddell 1990 ⁴
	G	Pos/Neg*	Native	Rainbow trout	Berejikian et al. 1996 ⁵
Predation	G	0	Non-native	Masu salmon	Reinhardt in press ⁶
	E	Neg	Native	Brown trout	Dellefors and Johnsson 1995 ⁶
	G	Neg	Native	Brown trout	Johnsson et al. 1996 ²
	G	Neg	Non-native	Rainbow trout	Johnsson and Abrahams 1991 ²
	G	Neg	Native	Rainbow trout	Berejikian 1995 ⁷
	G	Neg	Native	Brown trout	Fernö and Järvi 1998 ^{2,8}
	G	Neg	Native	Brown trout	Fernö and Järvi 1998 ^{2,8}

*Direction depended on age.

Comments regarding usage of data in meta-analysis:

¹P-value was calculated from data.

²P-value, given as < 0.05 or just “statistically significant”, was set to 0.05.

³P-value, given as > 0.6, was set to 0.61.

⁴Separate statistics were given for each of seven days of observations. Each of the *P*-values (range 0.9 - 0.001) was treated as independent.

⁵Separate statistics were given for each of three juvenile ages. These *P*-values were treated as independent.

⁶No statistics or raw data were available for inclusion of study.

⁷Separate statistics were given for two different test-environments. The two *P*-values were treated as independent.

⁸*P*-value for difference in “fleeing” was used.

ist. Tests for environmental effects compare fish, of a common origin, reared in a hatchery with those reared in the wild. By contrast, tests for genetic effects compare hatchery and wild fish reared from eggs in a common environment.

Because tests of differences are usually conducted under artificial hatchery conditions, their value for predicting effects of interactions in the wild may be somewhat limited. This may be particularly problematic if genotype/phenotype by environment interactions exist, whereby the relative expression of traits between the two types of fish differs among environments. Some stud-

ies try to control for such interactions by conducting tests under differing environments (e.g., hatchery and wild), yet most studies do not. Any lack of correspondence between hatchery tests and data from the wild, therefore, may be partly attributable to this problem.

Which characters differ?

Ecological interactions among fish are an outcome of their behavioural traits. Thus, knowledge about behavioural differences between hatchery and wild populations is vital to understanding

the potential impact from released fish. A substantial body of data that tests for such differences exists. These studies suggest that hatchery fish differ from wild fish in levels of aggression and predator avoidance behaviour (Table 1). In most studies, the effect of artificial rearing appears to result in an increase in levels of aggression (5 out of 9 studies). If we combine the probability values from the separate significance tests of the independent data sets (a meta-analytical approach described in Sokal and Rohlf (1981), p. 779; data handling described in footnotes to Table 1) these support the hypothesis that hatchery fish exhibit increased levels of aggression relative to wild fish ($\chi^2 = 85.75$, $df = 30$, $P < 0.001$).

Only in one study were the offspring from the wild population more aggressive than those from the hatchery population, and in this case, the hatchery population was of non-native origin (Norman 1987). Thus, population-specific levels of aggression rather than effects of hatchery-rearing may be responsible for the result (e.g. Taylor 1988, Swain and Holtby 1989, Einum and Fleming 1997). Finally, in one study the direction of the difference depended on the age of the fish, with wild fish being more aggressive at emergence, and hatchery fish being more aggressive after 105 days of rearing (Berejikian et al. 1996). In the three studies where the origin of the difference was predominantly environmental, hatchery fish were consistently more aggressive than wild fish. The less consistent results appear in those studies where the difference was genetic. There has been some debate as to whether artificial selection in fish causes an increase or a decrease in levels of aggression. Both theoretical and empirical studies suggest that the direction of selection during artificial rearing may depend on the environment (Doyle and Talbot 1986, Ruzzante and Doyle 1991). Although these studies have focused on situations where there is intentional selection for rapid juvenile growth, and thus may not be directly applicable to most hatcheries producing fish for stocking of wild populations, they suggest that a correlated increase in aggression only will result if food is

limited. Thus, if the environment to which fish are exposed differs among hatchery stocks this may influence the direction of evolutionary divergence of social behaviour away from that of wild fish. Nevertheless, increased aggression may evolve as a correlated response to selection for rapid growth, if such selection occurs (cf. Johnsson et al. 1996). Furthermore, evidence from guppies suggests that levels of aggression may be negatively correlated with predation rates (Endler 1995). Thus, if hatchery populations are less exposed to predators, phenotypic or genetic correlations may cause increased aggression as well. Tightly controlled experiments are needed to further elucidate the causal relations between feeding, growth, body size, aggression and dominance under various selective regimes.

Hatchery populations do differ from wild fish in levels of anti-predator behaviour (combined probabilities $\chi^2 = 37.63$, $df = 10$, $P < 0.001$). The lack of exposure to predators in hatchery populations appears to result in a reduced response to predation risk, both as an environmental effect and as a response to relaxed selection in hatchery populations (Table 1).

One intriguing feature of anadromous salmonids is their long distance migrations to feeding and breeding areas. As well as being energetically costly, such migrations potentially increase predation risk. Selection is therefore expected to mould patterns of movement to optimise fitness. It is therefore worrying that migration patterns of hatchery-reared fish often differ from those of wild fish (Table 2). For example, hatchery fish are observed to differ from wild fish in their timing of migration, which may influence both their susceptibility to predation and their energetic costs (i.e. due to different temperature and flow regimes). If this effect on timing of migration also influences breeding time, offspring survival may be compromised due to inappropriate emergence timing from nests (Einum and Fleming 2000b).

Hatchery populations may also differ from wild populations in feeding behaviour and habitat use (Table 3). However, results regarding such effects are more equivocal, potentially reflecting a time

Table 2. Movement patterns of pre-adults from hatchery populations of salmonids. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Origin of effect	Observations	Fish Origin	Species	Reference
E	Stay longer in sea.	Native	Arctic char	Finstad and Heggberget 1993
E	Extended period of smolting.	Native	Atlantic salmon	Hansen 1987
E	Differences in timing of recapture of hatchery and wild fish in coastal net fishery.	Native	Atlantic salmon	Potter and Russell 1994
E	Use same oceanic areas as wild fish.	Native	Atlantic salmon	Hansen and Jonsson 1991, Hansen 1988
E	Similar oceanic migration patterns.	Native	Atlantic salmon	Jonsson et al. 1990
E	Wild fry resided in estuary longer than hatchery fish.	Native	Chinook salmon	Levings et al. 1986
E + G	Juveniles enter estuary earlier than natural produced fry. Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Chum salmon	Lannan 1980
E + G	Earlier returns of adult fish to rivers in stocked streams.	Non-native	Coho salmon	Nickelson et al. 1986
E > G	Move more within stream.	Non-native	Brown trout	Bachman 1984
G	Low stamina during swim trials.	Non-native	Brook trout	Green 1964
G	Juveniles stay higher in water column.	Non-native	Brook trout	Moyle 1969
G	Juveniles tamer, surface oriented and lower stamina during swim tests.	Non-native	Brook trout	Vincent 1960
G	Juveniles stay higher in water column.	Non-native	Masu salmon	Reinhardt in press
G > E	Distance transferred from natal stream negatively related to recovery rate for hatchery reared fish.	Non-native	Coho salmon	Reisenbichler 1988

Table 3. Pre-adult feeding, habitat use and morphology of hatchery populations compared to wild fish. E = predominantly environmental, G = predominantly genetic, E + G = both environmental and genetic effects potentially important, E > G = likely predominantly environmental, G > E = likely predominantly genetic.

Trait	Origin of effect	Observations	Fish Origin	Species	Reference
Feeding	E	Different diet.	Native	Atlantic salmon	Reiriz et al. 1998
	E	Lower total consumption and feeding efficiency of live prey.	Native	Brown trout	Sundström and Johnsson in press
	E > G	Reduced feeding and diet width.	Native and non-native	Atlantic salmon	Sosiak et al. 1979
	E > G	Low feeding rate.	Non-native	Atlantic salmon	Fenderson et al. 1968
	E > G	Different diet initially, similar later.	Native and non-native	Brown trout	L'Abée-Lund and Langeland 1995
	E > G	Reduced feeding.	Non-native	Brown trout	Bachman 1984
	E > G	Different diet initially, similar later.	Non-native	Brown trout	Johnsen and Ugedal 1986, 1989, 1990
Habitat use	G	Similar diet.	Non-native	Brook trout	Lachance and Magnan 1990a
	E > G	No difference in habitat.	Non-native	Brown trout	Greenberg 1992
	E > G	Different habitat.	Non-native	Cutthroat trout	Mesa 1991
	G	Similar habitat.	Non-native	Brook trout	Lachance and Magnan 1990a
	G > E	Non-native use different habitat in lake.	Native and non-native	Brown trout	Hesthagen et al. 1995
Morphology	E	Different from wild.	Native	Atlantic salmon	Fleming et al. 1994
	E + G	Increased smolt and adult body size.	Native	Brown trout and Atlantic salmon	Peterson et al. 1996
	E + G	Hatchery populations more similar to each other than to wild populations.	Native and non-native	Coho salmon	Hjort and Schreck 1982
	E > G	Different from wild.	Non-native	Coho salmon	Taylor 1986
	G	Different from wild.	Native	Brown trout	Peterson and Järvi 1995
	G, E + G	Hatchery reared wild and hatchery population differed least. These differed substantially from wild reared wild population.	Non-native	Coho salmon	Swain et al. 1991

lag in adjustment to feeding on natural prey. Released fish may initially behave inappropriately after being introduced into a novel environment, but with time may acclimate to the local environment. For example, L'Abée-Lund and Langeland (1995) found that the diet of released brown trout initially differed from that of wild trout, but within the first summer the released fish adopted a similar diet (see also Johnsen and Ugedal 1986, 1989, 1990).

Hatchery populations may also differ morphologically from wild fish (Table 3). Salmonid populations exhibit differences in morphological traits, and these differences have been suggested to result from local adaptations to environmental conditions (e.g. Riddell and Leggett 1981, Riddell et al. 1981). Furthermore, morphological traits are important determinants of breeding success (Fleming and Petersson 2001). Thus, any deviation in morphology from the local population may be expected to result in decreased fitness.

How successful are hatchery fish in the wild?

If hatchery fish differ from wild fish in so many respects, how successful are the released fish likely to be in the wild? Assuming that the wild populations have undergone natural selection for ten thousand years (since end of the last ice age) to become adapted to the local environment (Ricker 1972, Taylor 1991), one would predict that these changes in fitness-related traits are a potential problem for released fish, and may influence their ability to survive and reproduce (see also Fleming and Petersson 2001). Their performance in the wild should therefore be expected to be inferior to that of wild fish, a pattern that is commonly observed (Table 4). In four of eight studies wild fish outgrew released hatchery fish, whereas the opposite was observed in two studies. Thus, although growth rates usually differ among hatchery and wild fish, the direction of this difference is not consistent (combined probabilities $\chi^2 = 4.07$, $df = 12$, $P > 0.99$). In contrast, hatchery fish consistently experienced reduced survival compared to wild fish (15 of 16 studies, combined probabilities $\chi^2 = 109.15$, $df =$

18, $P < 0.001$). Thus, the success of hatchery-produced fish after release appears to be constrained by phenotypic divergence from their wild conspecifics. This is not surprising given the potential importance of local differences among wild salmonid populations in fitness-related traits and the evidence we have presented concerning the effects of hatchery environments on development and selection.

How do naturally produced fish respond to released fish?

Given our knowledge about the performance of hatchery-reared fish in the wild, can we predict how stocking may influence the natural productivity of salmonid populations? How will ecological interactions with hatchery fish impact wild fish? For instance, if the fish we release into a river are more aggressive than the native fish, chances are that naturally produced fish are displaced from their territories during competitive interactions (Table 5). Such effects may be modified due to competitive asymmetries caused by prior residency or differences in body size (cf. Johnsson et al. 1999, Cutts et al. 1999).

One intriguing question arises from the observation that even though hatchery-reared fish appear to be more aggressive than wild fish, and thus should be able to displace them in territorial contests, they suffer higher mortality in the wild. Obviously, social hierarchies are not the only determinants of mortality rates in salmonids. Other factors such as response to predators and metabolic rate relative to food availability (i.e. vulnerability to starvation) may contribute substantially to mortality rates. One might speculate that hatchery fish are to some degree able to displace naturally produced fish, but that they are unable to cope with the high cost associated with this behaviour in terms of risk of starvation or predation. If so, net fish production may actually decrease as a result of stocking (cf. Fleming et al. 2000).

An additional number of potential effects can cause releases to have detrimental effects on wild fish. For example, released fish may influence the

Table 4. Pre-adult growth and survival of hatchery populations in the wild. E = predominantly environmental, G = predominantly genetic, E > G = likely predominantly environmental. Neg = hatchery fish inferior performance, Pos = hatchery fish superior performance, 0 = no observable difference.

Trait	Origin of effect	Form of effect	Fish origin	Species	Reference
Growth	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	0	Native	Atlantic salmo	Jonsson et al. 1991 ¹
	E	Pos	Native	Coho salmon	Irvine and Bailey 1992 ²
	E > G	Neg	Non-native	Brown trout	Hesthagen et al. 1999
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952 ³
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953 ³
	G	Pos	Native	Atlantic salmon	Kallio-Nyberg and Koljonen 1997
	G	*	Native	Rainbow trout	Reisenbichler and McIntyre 1977 ⁴
Survival	E	Neg	Native	Arctic char	Finstad and Heggberget 1993
	E	Neg	Native	Atlantic salmon	Hansen 1987 ⁵
	E	Neg	Native	Atlantic salmon	Jonsson et al. 1991
	E	Neg	Native	Chinook salmon	Unwin 1997 ³
	E	Neg	Native	Rainbow trout	Reisenbichler and McIntyre 1977 ⁴
	E > G	Neg	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999 ³
	E > G	Neg	Non-native	Brown trout	Kelly-Quinn and Bracken 1989 ³
	E > G	Neg	Non-native	Brown trout	Skaala et al. 1996 ³
	E > G	Neg	Non-native	Cutthroat trout	Miller 1953 ³
	E > G	Neg	Non-native	Cutthroat trout	Miller 1952 ³
	G	Neg	Non-native	Atlantic salmon	De Leaniz et al. 1989
	G	Neg	Non native	Brook trout	Flick and Webster 1964 ⁶
	G	Neg	Non-native	Brook trout	Lachance and Magnan 1990b ¹
	G	Neg	Non-native	Brook trout	Vincent 1960
	G	Neg	Non-native	Brook trout	Fraser 1981 ⁷
	G	**	Native & non-native	Brown trout	L'Abée-Lund and Langeland 1995 ³

*Hatchery/wild hybrids outgrew pure populations. ³No statistics or raw data were available for inclusion of study.
**Wild population intermediate survival of two hatchery populations. ⁴P-value was calculated from Table 4, comparing pure hatchery strain with pure wild strain.
Comments regarding usage of data in meta-analysis: ⁵P-value was calculated from data.
¹P-value was calculated from Table 3. ⁶P-value was calculated from Table 2.
²P-value was calculated from length data in Table 3. ⁷P-value was calculated from Table 4.

timing of migration of wild fish. Hansen and Jonsson (1985) suggested that wild smolts were attracted to shoals of released smolts and join them when migrating downstream. Furthermore, releasing fish may influence interspecific hybridisation rates. Jansson and Öst (1997) suggested that this was the reason for the high levels of hybridisation between Atlantic salmon and brown

trout observed in the River Dalälven, Sweden (41.5% hybrid parr). This may be of particular concern when species are extended beyond their natural range, where pre-zygotic isolation mechanisms against hybridisation with indigenous species may be absent (Leary et al. 1995). Releases of hatchery fish can also attract predators (including humans), and thus may cause the inten-

Table 5. Effects of stocking on wild populations.

Performance	Observation	Fish origin	Species	Reference
Productivity	Densities similar in stocked and unstocked sections of stream.	Non-native	Brown trout	Kelly-Quinn and Bracken 1989
	Spawning among hatchery reared and hybridisation with native population demonstrated. Survival rates of 0+ three times higher in native than in hybrids.	Non-native	Brown trout	Skaala et al. 1996
Growth	Movement of resident trout higher out of stocked sections.	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999
	Total population size unaffected by stocking.	Native	Chinook salmon	Unwin and Glova 1997
	No increase in total population size. Reduced natural production.	Native & non-native	Coho salmon	Flagg et al. 1995
	10-fold reduction in wild spawner densities, suggested to be result of hatchery selection for early spawning and displacement of wild fish.	Non-native	Coho salmon	Nickelson et al. 1986
	Total number of juveniles higher in stocked streams than unstocked one summer after stocking. Wild juveniles less abundant in stocked than unstocked areas. Similar numbers returned to spawn in stocked and unstocked, but lower density of resulting juveniles in stocked streams.	Native*	Rainbow & Brown trout	Vincent 1987
After stop of stocking, large increases in natural production of rainbow and brown trout. Stocking in previously unstocked stream caused reduced production of wild brown trout.	Non-native	Rainbow & Cutthroat trout	Petrosky and Bjornn 1988	
Stocking of high rates of rainbow (8-10 times wild density), but not lower rates, caused reduced survival of wild rainbow and cutthroat trout.	Native	Chinook salmon	Levings et al. 1986	
Residence time and growth in estuary unaffected by presence of hatchery fish.	Non-native	Brown & Rainbow trout	Weiss and Schmutz 1999	
Growth of resident brown trout unaffected. Resident rainbow reduced growth in stocked sections.	Native & non-native	Brown trout & Atlantic salmon	Jansson and Öst 1997	
Massive stocking of hatchery reared fish force salmon and trout to common spawning grounds, causing hybridization. 41.5 % hybrid parr in restored river section.	Native	Atlantic salmon	Hansen and Jonsson 1985	
Wild smolt attracted to shoals of released smolt and join them when migrating downstream.	Native	Chum salmon	Lannan 1980	
Long-term change in mean date of entry of adult fish after hatchery program initiated.	Native	Coho & Chinook salmon	Beamish et al. 1992	
Numerical response of spiny dogfish to stream mouth at time of hatchery release of smolt.	Native	Pacific salmon	Collis et al. 1995	
Squawfish aggregate to feed on hatchery-released juvenile salmonids.				

* Both brown and rainbow trout were historically non-native species in this system, but have now established self sustaining populations.

sity of predation on naturally produced fish to increase (Beamish et al. 1992, Collis et al. 1995).

While little is known about the level of early maturation as parr among hatchery-reared fish, it is likely that the high growth rates that they experienced in the hatchery will increase the potential for early maturation following release. If so, this will alter patterns of sexual selection in wild populations and may ultimately affect the adaptive landscape, leading to evolutionary responses in the recipient population (reviewed in Fleming 1998).

The effects that released hatchery fish can impose on naturally produced fish should make us cautious toward implementing stocking programs to compensate for habitat degradation and to increase fisheries. Indeed, under certain scenarios, theoretical models suggest that long-term stocking may lead to extinction of the native population (Evans and Willox 1991, Byrne et al. 1992). Existing empirical studies clearly show that fish density in stocked streams may not show the desired positive response to releases (Table 5). In fact, in some cases a negative trend in population density has been associated with releases. Perhaps the best evidence for such an effect comes from a controlled study where populations of coho salmon were monitored for five years in 15 stocked and 15 unstocked streams (Nickelson et al. 1986). Stocked streams had higher densities of juveniles after stocking, but the number of adults returning to the two types of streams did not differ. Furthermore, spawning success of released fish was reduced, causing a lower density of juveniles in the stocked streams than in the unstocked ones one generation later.

Conclusions

The performance of hatchery fish and their interactions with wild fish appear to be of such a character as to suggest that many of the current stocking practices may be detrimental to the recipient populations. The present synthesis should incite caution in our attempts to mitigate negative effects of habitat degradation by releasing hatchery-produced fish. Although the reports pub-

lished, and thus referred to here, may be biased towards negative effects of stocking, the potential for negative effects must nevertheless be acknowledged and dealt with.

A critical question we might ask ourselves is whether something can be done to avoid negative ecological effects of stocking? The answer to this question is yes and no. Better broodstock collection and mating protocols, more-natural rearing conditions, wild-fish-friendly release strategies and more focus on local broodstocks can improve the quality of hatchery fish released and reduce their impacts on wild fish. Behavioural deficits arise due to phenotypic responses to the radically unnatural abiotic and biotic environment of hatcheries, and will initially be environmental in origin but over generations of rearing will also involve genetic responses. Generally, hatcheries are psychosensory-deprived environments for fish (Olla et al. 1998). Adding complexity and enriching the environment is a common method for improving the well-being of captive animals (e.g., mammals, reptiles and birds) and may have application to hatchery populations of salmonids. Such an approach could reduce environmentally induced differences between cultured and wild fish, and increase post-release survival by decreasing stress, reducing domestication and acclimating fish more appropriately for their future environments (Berejikian et al. 2000). This could be done by adding habitat complexity, altering water-flow velocities, supplementing diets with natural live foods and reducing rearing densities to produce fish more wild-like in appearance and with natural behaviours and survival (Flagg and Nash 1999). For example, increasing habitat complexity has been shown to aid in the development of appropriate body camouflage colouration and increase behavioural fitness (Maynard et al. 1995). Similarly, anti-predator conditioning can improve post-release survival, as predator recognition and avoidance behaviour in juvenile salmonids improves in fish exposed to predators (Potter 1977, Olla and Davis 1989, Berejikian 1995) or odours from injured conspecifics (Brown and Smith 1998, Berejikian et al. 1999).

The development of release strategies that minimise negative ecological effects of hatchery fish on wild fish could also be a significant improvement. Released juveniles should be within the size range of wild juveniles, if not of a similar size distribution. The greatest risk of releasing large hatchery fish is that they may out-compete wild fish, endangering the natural production of the population. Releases of hatchery fish should also complement the natural spatial and temporal patterns of abundance of wild fish in the population. That is, the number of fish released should not exceed the carrying capacity of the environment, which varies spatially within the river and through time.

Thus improvement in the way hatchery fish are reared and released can lead to significant strides towards reducing their negative ecological impacts on wild fish. However, as Waples (1999) points out, it is a myth to believe that these changes will make the problems disappear altogether. This is because (1) environmental and genetic changes to fish in hatcheries cannot be avoided entirely; and (2) many of the risks are negatively correlated, so efforts to reduce one risk simultaneously increases another. Clearly we need to, first and foremost, be cautious in our use of hatcheries, particularly when releases are to be used in supplementing wild populations. We need to better understand how to culture fish for release (i.e. phenotypic responses to culture and effects of domestication, and how to minimise them) and how to release these fish to minimise/eliminate potentially detrimental impacts on wild populations while contributing to an overall increase in productivity.

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