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The future of stock enhancements: lessons for hatchery practice from conservation biology

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Abstract

The world's fish species are under threat from habitat degradation and over-exploitation. In many instances, attempts to bolster stocks have been made by rearing fish in hatcheries and releasing them into the wild. Fisheries restocking programmes have primarily headed these attempts. However, a substantial number of endangered species recovery programmes also rely on the release of hatchery-reared individuals to ensure long-term population viability. Fisheries scientists have known about the behavioural deficits displayed by hatchery-reared fish and the resultant poor survival rates in the wild for over a century. Whilst there remain considerable gaps in our knowledge about the exact causes of post-release mortality, or their relative contributions, it is clear that significant improvements could be made by rethinking the ways in which hatchery fish are reared, prepared for release and eventually liberated. We emphasize that the focus of fisheries research must now shift from husbandry to improving post-release behavioural performance. In this paper we take a leaf out of the conservation biology literature, paying particular attention to the recent developments in reintroduction biology. Conservation reintroduction techniques including environmental enrichment, life-skills training, and soft release protocols are reviewed and we reflect on their application to fisheries restocking programmes. It emerges that many of the methods examined could be implemented by hatcheries with relative ease and could potentially provide large increases in the probability of survival of hatchery-reared fish. Several of the necessary measures need not be time-consuming or expensive and many could be applied at the hatchery level without any further experimentation.

Keywords conservation biology, fisheries, hatcheries, reintroduction, restocking

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Introduction

The role of hatcheries in maintaining fish stocks

The world's fish species are under threat from habitat degradation and over-exploitation. In many instances, attempts to bolster stocks have been made by rearing fish in hatcheries and releasing them into the wild. In response to the rapid decline in fish numbers, hatcheries breed, rear and release billions of fish annually. It has been estimated (Welcomme and Bartly 1998) that well over 300 species worldwide are involved and every country contributes to some extent. Of these 300 or so species 290+ are freshwater (Welcomme 1992); therefore, marine stocking is still relatively uncommon. The amount spent annually on rearing and releasing hatchery fish is yet to be estimated, but there is little doubt that the total annual bill runs into billions of dollars. The number of hatchery-reared Atlantic salmon released every year, for example, is well over 5 billion. A conservative estimate of the number of hatchery-reared Atlantic salmon released in the UK during the year 2000 was around 8 million, 98% of which were released in Scotland. In 1996, Iran released over 12 million sturgeon (*Acipenser oxyrinchus,* Mitchill), 2.5 million perch (*Perca fluviatilis*), 100 million bream (*Abramis brama*, L.) and 140 million mahi sephid (*Rutilus frisii*, Nordmann) (Abdolhay 1996). These figures are almost certainly dwarfed next to the figures from North American, Japanese and Nordic regions (see Welcomme and Bartly 1998 for a review of the extent of fishery enhancements and Fushimi 2001 for a review of Japanese stock enhancement programmes specifically).

Despite these massive releases, in most cases there has been little change to the abundance of target species entering the fishery (Coleman *et al.* 1998; Svasand *et al.* 2000). With few exceptions, the results of restocking from hatcheries have either been poorly monitored or considered unsuccessful in the few cases where impact of release has been monitored (Svasand *et al.* 2000). Salvanes (2001), for example, questions the underlying assumption that humans have reduced many fish stocks below carrying capacity and that the release of captive-reared juveniles will lead to an increase in the number of adults and thus recruitment into the fishery. For the most part, scientific assessment of this assumption has been considered too difficult to address and has largely been ignored. In the case of marine species there is a scarcity of data relating to the movements of fish, natural mortality rates and most other aspects of their behaviour and ecology.

The first step in evaluating the success of a reintroduction programme aught to stem from biological/scientific studies (Lindburg 1992). These must estimate the survival of released fish, the principal causes of mortality, their contribution to subsequent generations (and resident gene pools), and perhaps even the impact on the environment as a whole. Secondly we may wish to determine if releases from hatcheries are economically feasible. If not, then it may be possible to alter hatchery practices in order to redress the balance. Recent studies into the enhancement of cod stocks (Svasand *et al.* 2000) and advances made in the Japanese flatfish hatchery programmes (Hossain *et al.* 2001) provide clear examples of how a greater scientific understanding of the behaviour and ecology of the species in question and long-term intensive monitoring provide greater insight into the shortfalls of hatchery programmes. Further, they provide clear suggestions as to how the efficiency of the industry can be improved and moved towards economic viability.

While restocking is widely used as a fisheries management tool, it has also been used for the conservation and management of threatened species (e.g. Flagg *et al.* 1995). In 1990, 27% of all federal recovery programmes for endangered freshwater fish in the USA included captive breeding as one of the recovery components (Andrews and Kaufman 1994). For example, steelhead trout (*Oncorhynchus mykiss*) were recently listed under the US Endangered Species Act and the recovery programme relies heavily on hatchery-reared individuals for restocking (Berejikian *et al.* 2000).

Restocking versus reintroduction

Fisheries management and conservation biology have remarkably similar agendas as both seek the long-term viability of fish stocks albeit for different reasons. Conservationists are interested in maintaining biodiversity whilst fisheries managers are interested in maximizing productivity. In the case of the conservation biologist, the establishment of self-sustaining populations in the wild is a principal objective. While this would also be ideal for fisheries managers, providing a stable return to the industry is a priority. In the former case, survival to reproductive age is imperative; in the latter, however, survival to a required size for capture is important and this size may or may not contribute to the establishment of self-sustaining populations. Conservationists may, therefore, be prepared to invest more time and money in the production of ecologically viable juveniles for release, but we emphasize that both groups should ultimately be looking to improve post-release survivorship.

Surprisingly, the practical methods utilized by each group are worlds apart, perhaps reflecting the difference in emphasis. Conservation biology has long emphasized the importance of practices such as environmental enrichment, pre-release training programmes and soft release to improve the post-release survivorship of captive-bred animals (see Beck *et al.* 1994 for summary statistics). In contrast, the production of ecologically viable individuals is not part of the hatchery equation because the production of large quantities of fish, rather than natural history, behaviour and ecology, largely guides hatchery practices (Johnsson 1993; Fushimi 2001). Agersborg (1934) states that rapid growth and high survivorship within the hatchery have been the fundamentals of aquaculture for years. This position still reigns supreme today. Many hatcheries are government funded or at least heavily subsidized. The level of success, and hence funding is often being determined by the number of fish released rather than by the survival rates of those fish or the return to anglers and the industry.

Hatchery shortfalls

While hatchery-rearing techniques have been perfected over the last few decades and continue to provide more and more fish for release, the proportion of fish surviving to adulthood is in decline (Nickleson 1986; Beamish *et al.* 1992; Pearcy 1992; Coleman *et al.* 1998; Blaxter 2000). In the case of salmonids typically, less than 5% of all hatchery-reared fish make it to adulthood (McNeil 1991). In UK, the number is more likely to be below 3% and for many other species released from hatcheries the figure is commonly far lower (e.g. chum salmon 1–3%, and <1% for cod; Salvanes 2001). At first glance these statistics seem little different from the rates observed in wild fish. However, if we examine age-specific mortality, bearing in mind that most species are reared in captivity for extended periods and released between 6 months and 2 years of age, then we see that captive-reared fish do very poorly indeed (Reisenbinchler and McIntyre 1977; Chilcote *et al.* 1986; Leider *et al.* 1990). It has been estimated that the mortality rate of released cod is at least twice that of wild juveniles (Svasand *et al.* 1989). Captive-reared Japanese flounder (*Paralichthys olivaceus*) also show massive levels of mortality in the first few days after release (only 10% make it to 10 days post-release) primarily due to the loss of fish that lack appropriate pigment patterns (Blaxter 2000) and inappropriate antipredator responses (Furuta 1996). Even when age-specific mortality is not taken into consideration, Wiley *et al.* (1993) suggest that stocked fish still show lower survival from eggs to catchable sizes than their wild counterparts. Most of the mortality occurs in the first few days following release rather than over the subsequent months (Howell 1994; Blaxter 2000; Svasand *et al.* 2000). These figures are exactly what one would expect given the methods currently employed during hatchery rearing and release and are indicative of predator-mediated mortality. If hatchery-reared fish manage to survive their first week or so in the wild, then the chance of long-term survival is greatly increased (Kanid'hev *et al.* 1970; Brown and Smith 1998). This brief time following release represents a prime target period towards which future research efforts should be directed.

The relatively poor success rate of restocking and various other environmental issues (for example, loss of genetic integrity of wild stocks) have led to a fierce debate regarding the value of hatchery supplementation programmes (see Winton and Hilborn 1994 for further discussion). It is worth highlighting the fact that hatcheries must give careful consideration to the choice of brood stock if genetic 'pollution' of the resident wild stock is to be prevented (Utter 1998; Doyle *et al.* 2001). Ideally, a large number of mature individuals should be sourced from the target population every year. In some instances (e.g. salmon hatcheries in UK), brood stock are captured during local spawning runs every season, but this appears to be the exception rather than the rule. In contrast, managers working on the conservation programme for the Mary River cod (*Maccullochella peelii*) in Australia go to a considerable effort to maximize the genetic diversity by constantly turning over the brood stock (Simpson and Jackson 1996). Releases of fish species outside their natural range (introduction as opposed to reintroduction) for fisheries purposes aught to be strongly discouraged or at the very least strictly controlled. Although the IUCN guidelines for the translocation of animals do not have the scope to address the introduction of exotic species for fisheries purposes, they do nevertheless provide a reasonable lead as to the types of issues that aught to be addressed prior to introduction.

All other issues aside, there is little doubt that poor survival of hatchery-reared fish is a major concern as it greatly reduces the efficiency of using hatchery stocks to supplement wild production whether for commercial or conservation means (Mesa 1981; Sproul and Tominaga 1992; Maynard *et al.* 1995; Olla *et al.* 1998). Nevertheless, hatchery supplementation of wild stocks looks set to play a major role in maintaining the sustainability of many fisheries stocks for the foreseeable future. Furthermore, restocking or reintroduction programmes seem set to aid in the conservation management of endangered fish species especially when utilized in concert with habitat preservation and restoration (e.g. Secor and Houde 1998). Finally, releasing fish into the wild knowing they are totally unprepared for survival and the majority will die, presents a considerable ethical conundrum that ought to be addressed. In order to move forward the focus of hatchery management must now switch from husbandry to improving the post-release survival chances of hatchery-reared fish.

Identifying specific problems

Fisheries biologists have known for years that hatchery-reared individuals show substantial deficits in virtually all aspects of their behaviour (see Stone 1872 and Lord 1934 for example). As early as the forties, Fish (1940) recognized that hatcheries circumvented natural selection in order to artificially boost hatchery survival. Arguably the two most important behaviours any animal must develop are the ability to eat and avoid being eaten. Early attempts to raise enough wild prey to maintain hatchery populations proved impossible and the focus quickly turned to developing artificial food sources (Embody and Gordon 1924). Hatchery-reared fish are now routinely reared on a mundane diet of man-made pellet foods that require limited use of potential foraging behavioural repertoires as there is no variation in the timing, location, abundance or type of food on offer. Hatchery-reared Japanese flounder, for example, are fed at the surface, which induces an unnaturally high level of 'off the bottom swimming activity' post-release, thus increasing their susceptibility to predators (Furuta 1996).

Laboratory experiments show that foraging behaviour is reliant on learning from prior experience (e.g. Paszkowski and Olla 1985; Stradmeyer and Thorpe 1987; Reiriz *et al.* 1998). Learning enables individuals to improve their prey recognition, attack mode and handling efficiency and is especially important when foraging in the wild as it can improve foraging efficiency by adjusting foraging behaviour to match contemporary circumstances (Hughes *et al.* 1992). These foraging behaviours are particularly important when the distribution, abundance and trophic value of prey are variable. Little wonder then, that upon release, hatchery fish often show dramatic deficits in their foraging behaviours. Following release many captive-reared fish may not eat at all for several days (Paszkowski and Olla 1985), weeks (Miller 1954) or up to a month (Usher *et al.* 1991). When they do start to forage, they typically take up high risk and energetically costly positions close to the surface of the water and in regions of high flow (e.g. red drum (*Sciaenops ocullatus*): Stunz *et al.* 2001). They often fail to disperse, are less aggressive and consequently are frequently found in unsustainably high densities having to compete heavily for limited resources (Olla *et al.* 1998). Often the released fish show limited prey choice, take fewer items and are very slow to switch between prey types compared with wild fish (Sosiak *et al.* 1979; Ersbak and Haase 1983). As a result hatchery-reared fish show substantial weight loss compared to transplanted wild fish and their mortality rates can be up to 10 times greater than that of wild fish (Miller 1954).

As with foraging behaviour, the antipredator behaviours of hatchery-reared fish are equally poorly developed and insufficient to cope with life in the wild. Fish reared in captivity are completely predator naïve because they are provided with no opportunity to interact with predators prior to release. Predation is thought to be the principal cause of mortality among released hatchery fish (Howell 1994); however, fish weakened by starvation are also more prone to risk taking and likely to fall victim to predation. There are three key behaviours that are important to develop if predator-induced mortality is to be reduced. The first involves avoidance strategies that reduce the probability of encountering predators (e.g. avoiding dangerous microhabitats, behaving cryptically or taking on cryptic colouration). The second is predator recognition and detection and the final behaviour is the antipredator response (schooling, fleeing to refuge, etc.) Like foraging behaviour, there is ample evidence that antipredator behaviour improves considerably with experience (Kanayama and Tuge 1968; Fraser 1974; Olla and Davis 1989; Csanyi and Doka 1993; Jarvi and Uglem 1993; Berejikian 1995; Brown and Smith 1996; Mirza and Chivers 2000; Hossain *et al.* 2001). Prior exposure is therefore vital to the development of effective antipredator behaviours and the improved viability of restocking procedures.

Finding a solution

In the process of addressing the problem of post-release mortality, much can be gained by reviewing the conservation biology literature. There are now numerous texts available that highlight the importance of ecology and behaviour in conservation management and more specifically in reintroduction biology (Olney *et al.* 1994; Clemmons and Buchholz 1997; Caro 1999a; Gosling and Sutherland 2000). One of the key aspects of a successful reintroduction is to ensure that the rearing environment is such that near-natural behaviours can develop during the period of captivity (Carlstead 1996; McLean 1997). The conservation of behavioural diversity should not be neglected (Buchholz and Clemmons 1997) especially in species where different populations exist that inhabit slightly different environments (e.g. salmon runs). Generally speaking, providing that husbandry techniques are good and result in healthy young then survival in captivity is guaranteed. If, however, the intention is to release the animals into the wild, behavioural considerations rather than husbandry must become a priority (Wallace 2000). Olla *et al.* (1994) suggested that it is 'critical . . . to develop methodologies for hatcheries to improve post-release behavioural performance'.

As early as 1965 it was recognized that fisheries research ought to be redirected at reducing post-release mortality rather than continuing to focus on mass production and release (Haskell 1965). Ultimately the aim of the hatchery should be to produce animals that are behaviourally, morphologically, physiologically and genetically similar to those in the wild (Brown and Laland 2001; Fushimi 2001). For the most part, selective breeding has effectively resulted in the production of domesticated strains of fish that are well adapted to life in captivity, which is far removed from the selective pressures of life in the wild. The development of behavioural patterns is heavily dependent on the ongoing and complex interaction between the environment and an individual's genotype (Alcock 1993). Those behaviours that rely on this interaction cannot develop correctly if the rearing environment differs to that in which the animal is destined to be released. It follows quite naturally therefore, that development in a dull, artificial rearing environment will result in individuals who are unprepared for life in the wild (Derrickson and Snyder 1992).

There are at least six major areas of behaviour that should be considered in the development of any scheme whose ultimate aim is release into the wild (Kleiman 1996). To survive candidates for reintroduction must be able to (i) avoid predators; (ii) acquire and process food; (iii) interact socially with conspecifics; (iv) find or construct shelters or nests; (v) locomote on or in complex terrain; and (vi) orientate and navigate in a complex environment. Thus, in order to design more natural rearing environments it is essential to have a broad understanding of the biology and ecology of the fish species in question and especially of the environment into which the animal is to be released (Kleiman *et al.* 1994). For the most part, these details are likely to be not only species- but also case-specific. For example, it is vital to know the types of predators and food items the individual is likely to encounter at the site of release. These details are likely to show considerable geographical variation even within a catchment. The degree of sociality may also play a considerable role in the success of release programmes (Wallace 2000). Prior social experience can have significant influences on future levels of aggression and dominance rank (Hojesjo *et al.* 1998). Many fish species are highly social and form shoals or schools for some or most of their lives. Others, however, are more solitary and may defend territories. In the former case, release in large groups would provide the best results, but for the latter, scatter seeding would be a better approach. For those species that have more complicated social relationships, such as the development of harems, density- or size-dependent hermaphrodites, etc., more attention must be paid to the demographic composition of the release groups.

For some fish early exposure to appropriate cues during sensitive periods at some stage in development is essential for ensuring appropriate behavioural responses later in life. Whilst imprinting (Lorenz 1952) has been shown to be extremely important in the social welfare of birds (Bolhuis 1991) and in reintroduction techniques (e.g. Wallace and Temple 1987; Lewis 1990), less is known about these periods in fish. Habitat imprinting is well known in salmonids that imprint on the chemical cues in their natal streams during critical stages of their development and later use these cues to navigate their way back to natal streams in order to breed. It seems likely that eels may rely on similar techniques. Less is known about sexual imprinting in fish but evidence from those fish that have some degree of parental care suggests that early exposure to appropriate 'sexual models' provides later guidance during mate choice (Weber and Weber 1976). Species cross-fostering experiments seem to indicate that exposure to sexual models may even be important in fish that do not show parental care (Korner *et al.* 1999). In these cases familiarity appears to play a large role in a fish's choice of social and sexual partners. These considerations are especially important if released fish are going to go on and breed in the wild, thus amplifying the initial investment in pre-release training whilst forming a self-sustaining population.

Management techniques

The conservation reintroduction literature suggests three principal management techniques, the implementation of which is recommended for a successful reintroduction programme. In most cases some combination of each of these three techniques is utilized. Determining the relative merits of each is often difficult particularly when working with endangered mammals or birds. Working with fish, however, should provide the ideal opportunity to assess the relative importance of each technique because of the large number of individuals that can be released. Such an experimental approach to assessing reintroduction techniques has long been called for by conservation biologists (Lindburg 1992; McLean 1997; Caro 1999b; Wallace 2000) and may provide useful information for all endangered species programmes.

Environmental enrichment

Environmental enrichment has come to mean many things in the reintroduction literature. It can simply mean increasing the structural complexity of the environment to relieve boredom or to provide a taste of the habitat the animal is likely to be exposed to in the wild (Shepherdson 1994; Miller *et al.* 1996). For example, lion tamarins (*Leontopithecus* sp.) have been given an opportunity to move around on natural vegetation prior to release (Beck *et al.* 1991) and providing wild cats with live fish or hidden food encouraged natural predatory tendencies and substantially reduced stereotyped pacing (Shepherdson *et al.* 1993).

For the most part, hatchery environments are completely devoid of structure. They tend to comprise of a featureless, monotonic enclosure with no opportunity to escape from conspecifics or display any other natural behaviour. They bear no resemblance whatsoever to the fish's natural environment and densities can be up to 100 times greater than those in nature. Reductions in density alone seem to have mixed results on post-release survival but it appears that intermediate densities produce better quality fish (Wiley *et al.* 1993). Many of the captive-breeding programmes for mammals allow the animals to experience realistic natural environments, or at the very least alternative habitats that contain some naturalistic features of the environment into which the animals are to be released (e.g. Beck *et al.* 1991; Biggins and Thorne 1994). Preliminary work where hatchery-reared fish are released into outside ponds prior to release suggests that brief exposure to this type of naturalistic environment improves survival rates substantially (e.g. Maynard *et al.* 1996). Naeslund (1992) found that brown trout (*Salmo trutta*) reared in outside ponds survived better when released into streams than standard hatchery-reared fish. In these situations the fish are not only exposed to natural temperature and light fluctuations and more complex habitat structure, they are also exposed to limited supplies of live prey and avian predation pressure. Similarly, fish provided with some cover in the hatchery showed increased growth and survival within the hatchery (Leach 1926).

These types of enrichment are likely to translate to greater survival post-release. Providing submerged structure creates visual isolation amongst potential competitors allowing the establishment of territories through improved visual references, leading to lower levels of aggression and improved growth rates (Mesick 1988). It has previously been suggested that simple measures like increasing flow rates within races to match wild conditions, providing dark backgrounds, semi-natural stream beds, submerged structure, and overhead cover could improve survival rates upon release (Leonard and Cooper 1941; Ritter and MacCrimmon 1973; Leon 1975; Butler 1981; Howell and Baynes 1993; Wiley *et al.* 1993; see Maynard *et al.* 1995 for a review). For example, Howell (1994) suggests that reduced opportunity for exercise in hatchery conditions leads to a reduced ability to flee from predatory strikes. Whilst Berejikian *et al.* (2000) found that steelhead trout provided with an enriched environment in the form of in-water structure, under-water feeders and overhead cover achieved a higher social rank and growth rate when mixed with conventionally reared fish.

Life-skills training

Life-skills training provides training regimes designed to alter the nature of an animal's behaviour or teach essential life skills (Brown and Laland 2001). Many behaviours require some degree of learning (see McLean 1997 for a review of learning and relevance to conservation reintroductions), which can only come about by repeated exposure to appropriate stimuli. In some animals social learning, for example via parental guidance, is necessary for the development of behaviours. Social guidance is particularly important in long-lived, highly social animals such as primates (Mineka and Cook 1988; Box 1991), elephants (Schulte 2000) and killer whales (Guinet and Bouvier 1995); however, it is by no means restricted to these taxa. Recent investigations into the occurrence of social learning suggest that it is a common and widespread phenomenon among many social species and is by no means restricted to 'higher order' or more 'clever' species. In fact, there is ample evidence that social learning plays a role in the development of many behaviours amongst fishes (Suboski and Templeton 1989; Brown and Laland 2001). Housing captive-reared individuals with more skilled conspecifics to demonstrate behaviours that are important to survival is a common reintroduction training technique (Kleiman 1989; Dobrott 1993).

Irrespective of the mode of learning, prior exposure to live prey (Morgan-Davies 1980; Phillips *et al.* 1995; Vargus and Anderson 1998) and potential predators (Carpenter *et al.* 1991; Maloney and McLean 1995; McLean *et al.* 1996; see Griffin *et al.* 1999 for a review) is a common practice in most conservation reintroductions, yet there are only a few studies investigating these types of experiences in hatchery-reared fish and the effect it might have on post-release survival (Jarvi 1990). Even if nonlive prey is provisioned, it may be hidden or embedded thus encouraging the animals to work for their food and in this way they may be primed to actively search for and catch live prey upon release. For example, swift foxes (*Vulpes velox*) were pre-adapted to natural foods by being provided with road-killed ungulates rather than pre-prepared meat (Scott-Brown *et al.* 1986). When food is added to the hatchery enclosure, limited searching is required to discover it, thus providing no opportunity for the fish to develop natural foraging behaviours.

It would be relatively easy to stimulate foraging behaviour in fish, without the use of expensive live bait, by using similar techniques as those outlined above. Alternatively, live prey may be introduced periodically or just prior to release to provide the fish with limited foraging experience with minimal time and monetary cost.

In fact, improvements in foraging behaviour have been shown to occur with repeated exposures (Godin 1978; Ringler 1979; Paszkowski and Olla 1985; Stradmeyer and Thorpe 1987; Reiriz *et al.* 1998). Improvements can be made in prey recognition, handling and selection (Ware 1971; Croy and Hughes 1991; Hughes *et al.* 1992). More complex foraging behaviours such as weighing up the costs and benefits associated with foraging under different levels of predation threat (Dill and Fraser 1984; Metcalf *et al.* 1987; Gotceitas and Godin 1993) and selective foraging based on trophic value and abundance can also be improved with experience (Hughes *et al.* 1992; Provenza and Cincotta 1993; Reiriz *et al.* 1998).

As early as 1966, Thompson (1966) was conducting experiments to determine if coho (*Oncorhynchus kistuch*) and chinook salmon (*O. tschawytcha*) could be conditioned to avoid a model predator by using electric shocks as negative stimuli. Subsequent tests conducted in large aquaria containing live predators showed that conditioned fish had a 50% increase in survival rate compared with control groups. Other studies conducted by Kanayama (1968) on chum salmon (*O. keta*) and Ginetz and Larkin (1976) using sockeye salmon (*O. nerka*) showed similar results. Experiments conducted by Olla and Davis (1989) found that prior exposure to a predator increased survival rates substantially on subsequent exposure (see also Hossain *et al.* 2001). It is now well established that prior experience with predators greatly improves antipredator responses in fish (Olla and Davis 1989; Magurran 1990; Kieffer and Colgan 1992; Jarvi and Uglem 1993; Berejikian 1995; Brown and Smith 1998; Brown and Warburton 1999). Fish may even show improved survivorship simply by interacting with predator-experienced individuals (see Patten 1977; Suboski and Templeton 1989; Wiley *et al.* 1993; Brown and Laland 2001). Jarvi (1990) showed that acclimation by Atlantic salmon to salinity levels and predators reduces stress and increases survivorship. Similarly, Jarvi and Uglem (1993) exposed hatchery-reared Atlantic salmon to cod either behind a partition or allowed them to directly interact with the hunting predator. In both instances antipredator responses were more appropriate than control groups on later exposure.

Both Suboski and Templeton (1989) and Brown and Laland (2001) suggest that foraging and predator avoidance training regimes could be implemented at the scale required for hatcheries. Certainly the pattern of post-release mortality observed in released fish implies that pre-release training should occur relatively quickly, as those that do survive the early post-release period must have rapidly acquired the necessary life skills in order to survive. This line of evidence combined with avoidance retention experiments (Brown and Smith 1998; Berejikian *et al.* 1999) suggests that pre-release training would not have to be an extensive, time-consuming process and providing that sensitive periods for learning are not jeopardized, need only be initiated shortly before release. Even a single exposure to predators may make a substantial difference to the behaviour of prey on subsequent exposures (Olla and Davis 1989; Pyanov 1993; Hossain *et al.* 2001)

Hard versus soft release

For the most part, traditional hatchery release practices transport the fish in large drums and simply dump the fish directly into the water body to be stocked. This process is often referred to as 'hard release' in the conservation biology literature. In stark contrast, many conservation programmes rely on a protocol called 'soft release'. In some cases the term 'soft release' has been used more broadly referring to the provision of any kind of training or preparation for release (pre- or post-release conditioning: Scott-Brown *et al.* 1986). Here we use the term far more restrictively referring solely to the practice of providing an acclimatization period at the release site (or close by) prior to liberation.

Soft release enables the animals to become accustomed to the prevailing environmental conditions (temperature and chemical composition of the water, for instance), familiarize themselves with local landmarks for orientation and navigation, recover from transportation, and develop cohesive social bonds wherever appropriate. For example, in the red wolf (*Canis rufus*), animals that survived for the longest periods of time following release were those who had experienced longer acclimatization periods (Phillips *et al.* 1995). Reports of disorientation following 'hard release' are common in the conservation biology literature (Kleiman *et al.* 1986). Vincent (1960) estimated that 10% of released fish appeared to be disorientated upon release, swimming into rocks, sandbars and even out of the water.

There is, however, already good evidence that an acclimatization period would greatly enhance hatchery fish survival upon release. It has been reported that coho smolts given less than 90-min recovery time showed lower survival rates than unstressed control groups (Olla *et al.* 1992), whilst Lagardere *et al.* (1988) and Goodyear (1973) both suggest that it takes around 3 days for fish to familiarize themselves with their new environment. Such familiarization can have unexpected benefits. For example, guam (*Rallus owstoni*) held in staging pens to adjust to the climate also benefited from natural prey passing freely through the pens providing them with time to acquire an appropriate search image whilst being protected from predation (Derrickson 1986). Also, preliminary studies suggest that if brown trout are held in enclosures in the river for 6 days at the site of release, prior to liberation, growth rates and recapture rates can be significantly improved (Jonssonn *et al.* 1999). Similarly, holding brown trout in enclosures for 24 h at the site of release had a positive effect on the number of fish recaptured (Cresswell and Williams 1983).

There is a large body of evidence showing that transportation has a significant effect on the stress levels of hatchery fish. Importantly, elevated stress levels have been associated with increased susceptibility to predators (Olla and Davis 1989; Jarvi 1990; Lepage *et al.* 2000), a reduced ability to learn (Olla *et al.* 1992), increased susceptibility to infections (Shepherd and Bromage 1992), changes in social behaviour (Ejike and Schreck 1980) and a reduced ability to cope with fluctuations in temperature and water chemistry (Strange *et al.* 1978). Physiological recovery from chronic stress is fairly rapid, occurring over a matter of hours; however, recovery of behavioural traits like aggression, territoriality and learning ability probably takes several days to weeks (Schreck *et al.* 1997). The length of time allowed for acclimatization, therefore, is likely to be positively correlated with improved survival for the short term (up to 7 days), but as time goes on negative effects (such as density-related aggression and reduced dispersal) may begin to offset the benefits of prolonged containment (Kaya and Jeanes 1995). Allowing an intermediate acclimatization period prior to liberation should, therefore, result in substantial reductions in post-release mortality. The exact length of acclimatization time required to maximize survival is again likely to be species- or case-specific and would be a profitable field for further experimentation.

Lessons learnt from hatchery releases

Release site characteristics

For the most part, much is already known about choosing the right location and the time of year for the release of captive-reared fish especially with reference to flow rates, habitat quality (including stream-bed structure), prey, predator and competitor abundance, etc. (Leber *et al.* 1996; Jokikokko 1999; see Cowx 1998 for a review). There are excellent recommendations set out by the IUCN as to when, where and how reintroductions should occur (IUCN/SSC Guidelines for Reintroductions 1995; and IUCN Position Statement on Translocation of Living Organisms 1987). We would, however, like to draw the reader's attention to the IUCN directives of reintroduction and restocking protocols (IUCN 1995, 1987, respectively) and suggest that these guidelines could certainly be helpful when establishing how best to release hatchery-reared fishes. In light of the abundant information already available on this topic we shall address this issue somewhat superficially paying particular attention to the potential complications of the existence of a remnant resident population, because success rates of hatchery releases are often correlated with the existence of resident populations (Welcomme and Bartley 1998).

The existence of a resident population often suggests that supplementation may be less successful due to further complication of social interaction of the resident and introduced fish. Laboratory studies suggest that hatchery-reared fish may be more aggressive than their wild counterparts (Swain and Riddell 1990; Berejikian *et al.* 1996), leading to the concern that hatchery fish could potentially displace wild stocks (see Nickelson *et al.* 1986). However, prior residency conveys an advantage to the resident during aggressive interactions (Caballero and Castro 1999; Volpe *et al.* 2001), possibly accounting for the lack of evidence that displacement actually occurs in the wild (Deverill *et al.* 1999). With few exceptions, hatchery releases continue to fail to make substantial contributions to resident populations possibly due to their inability to cope with competition from residents and the high levels of mortality that they sustain (Fenderson and Carpenter 1971; Bachman 1984). The provision of habitat enrichment during rearing at the hatchery may provide the key to the development of more natural social behaviours that could potentially alleviate some of the social inadequacies displayed by hatchery fish.

The absence of a resident population, on the other hand, may be indicative of an unsuitable reintroduction site as it suggests environmental degradation or extreme fishing pressure (see the reintroduction efforts of sturgeon in Chesapeake Bay for example: Secor *et al.* 2000). In these cases, it may be pertinent to address habitat restoration issues in concert with a reintroduction effort. From a conservation management perspective it is important to firstly manage any threatening processes prior to reintroduction or restocking (IUCN 1987, 1995). In the case of fisheries, however, the threatening process (i.e. fishing) is encouraged and may be the sole reason why the restocking is taking place and, ironically, may be funding it.

Size at release

The few studies that have monitored the survival rates of hatchery-reared fish all seem to come to the same conclusion: the size of the fish at release is a critical factor in determining the probability of survival. Generally larger fish have a higher survival rate. Mortality of small cod (<25–30 cm) is responsible for the decrease in numbers of released fish (Svasand *et al.* 2000). When juvenile Japanese flounder are released, they typically range from 4 to 12 cm long and only those larger than 9 cm survive and go on to grow to a commercial size (Masuda and Tsukamoto 1998). Similarly, red sea bream over 4 cm at release go on to contribute to the catch (Tsukamoto *et al.* 1989). A recent review of inland fish stock enhancement in

China suggests that grass carp greater than 10 cm in their second year of life have a much greater chance of survival (Li 1999). It is because of this size-correlated mortality that hatcheries grow fish in captivity for extended periods prior to release. However, the size at which fish are released is also governed by economic constraints. The longer the fish remain in captivity the greater is the cost to feed and house them. These extended grow-out periods also have strong adverse effects on the behaviour of the fish (as outlined above). Therefore, a balance must be found between the benefits of long-term captivity on mortality and the disadvantages of behavioural deficits. Pre-release training can address this problem to some extent, but work in this area is still very much in its infancy (Jarvi and Uglem 1993; Wiley *et al.* 1993; Brown and Smith 1998; Brown and Laland 2001) and has yet to be applied on a large scale.

Economic feasibility

There are currently few examples of restocking that are considered an economic success although the majority have yet to be fully assessed. Inland stocking, particularly in Asia, is often earmarked as a prime example of the success of stocking. Many examples of stocking in reservoirs and ox-bow lakes are often referred to as 'cost-effective' (Welcomme and Bartley 1998). Thai reservoirs, for example, are heavily stocked and the stocked fish are thought to contribute to $2 million worth of carp captured each year. Closer inspection, however, reveals that the relative contribution of the stocked fish to the fishery has not yet been evaluated (Bhukaswan 1988, cited in Welcomme and Bartley 1998). Only the chum salmon and perhaps the red sea bream (*Pagrus major*) release programmes, in Japan, appear to have been economically successful, primarily because the cost of production is so low. Even the salmon success may, in fact, have resulted from improvements in oceanic conditions because similar increases in populations that are not supplemented from hatcheries have been observed in North America (Bigler *et al.* 1996).

From a purely economic perspective, increased returns to the fishery would offset some of the costs associated with improving production and release methods similar to those outlined above (Behnke 1989). For example, if the probability of post-release survival could be doubled by changing rearing or releasing protocols at a cost of halving the total output of hatchery-reared juveniles, then such improvements should make little difference to the economic viability of hatcheries. With this in mind, hatcheries in Japan are now beginning to shift their focus towards producing fewer, higher quality juveniles for release (Fushimi 2001).

Models investigating the economic feasibility of releasing hatchery-reared cod indicate that in order to break even, a survival rate (i.e. survival until recruitment into the fishery) of 28% is required if 36-week-old juveniles are released (Wilson *et al.* 1998). This figure is far beyond anything that has been realized to date, although Kristiansen (1999) reports survival rates of 23% in the first year if juveniles are released at 23 cm. Perhaps the introduction of the techniques discussed above could close the gap between current survival rates and those required in order to break even. The economic data for the fishing industry as a whole suggests that economic success can hardly be considered a fair benchmark with which to judge the economic validity of altering restocking practices. Given people's insatiable appetite for fish, one must consider how much we are willing to pay for the continued privilege of catching and eating wild fish.

Conclusion

Fisheries scientists have known about the deficits in behaviour of hatchery-reared fish and the resultant poor survivorship in the wild for some time. Whilst there remain considerable gaps in our knowledge about the exact causes of post-release mortality, it is clear, based on our current level of understanding, that significant improvements could be made by rethinking the ways fish are reared, prepared for release and eventually liberated. The conservation reintroduction literature provides a guide as to the types of protocols that could be tested by fisheries researchers, and the data from fisheries releases could provide important feedback into the design of reintroduction programmes.

Improving fish culture methods should be considered a priority for future restocking programmes, both for fisheries and conservation purposes. The smallest improvements in the proportion of fish surviving to adulthood could result in substantial gains in absolute numbers of individuals entering the fishery. These gains would offset any increase in the price of production resulting from improved techniques such as environmental enrichment, life-skills training, or soft release. Many of the suggestions outlined above could be implemented relatively easily and may provide large improvements in post-release survival. The necessary measures need not be time-consuming or expensive.

Available data indicate that any training procedures need only be short-lived due to the rapid learning and reasonable retention periods displayed by fish. This suggests that training could take place in a brief bout just prior to release, periodically during development, or even in an acclimatization holding pen at the release site. The benefits of simple habitat enrichment procedures are already clear to see in the conservation and fish literature, and should soon be implemented by hatcheries on a large scale. The shoaling behaviour of some species of fish makes it possible to take advantage of social learning processes in order to increase the efficiency and efficacy of any training methods. Finally, we highlight the need for a greater understanding of the behaviour and ecology of commercial species and call for closer monitoring of hatchery releases so that their success may be gauged and areas for fertile future research brought to light.

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