© 2010 Universities Federation for Animal Welfare The Old School, Brewhouse Hill, Wheathampstead, Hertfordshire AL4 8AN, UK Animal Welfare 2010, 19: 139-149 ISSN 0962-7286

Aquaculture and restocking: implications for conservation and welfare

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Abstract

As the harvesting of fish through commercial fisheries becomes both harder and less economically viable, the world is becoming increasingly dependent on aquaculture to provide fish for human consumption. The closely related activity of stock enhancement, whereby large numbers of fish are reared and then released, is a common practice aimed at increasing the numbers of fish in rivers and along coasts. Aquaculture and stock enhancement practices raise a number of welfare and conservation issues both for fish that are reared within captivity, and for the local populations and habitats that are influenced by fish-rearing activities. In this review, we illustrate how fish farms and hatcheries have directly affected fish welfare. Examples cover on-farm fish husbandry and healthcare, the interactions between farmed and wild fish, and survival of fish released for stock enhancement. These aspects are often intertwined with important conservation issues. Thus, we also review direct effects that aquaculture-generated pollution can have on local habitats, issues associated with feeding reared fish, and problems created by alien fish (either escapees or intentionally released fish). While awareness of fish welfare is certainly growing, so is the rate at which fish are reared. There is, therefore, a pressing need to understand the welfare and conservation issues that are affected by aquaculture and stock enhancement.

Keywords: animal welfare, aquaculture, conservation, fish farming, restocking, stock enhancement

Introduction

Aquaculture is a rapidly growing industry whereby aquatic organisms are cultured for human consumption. It is often considered to be a modern industry designed to massproduce fish protein, but its roots go back several millennia. For example, there are references to the use of sluices and fish ponds in the Bible (Isaiah, chapter 19, verse 10), and there is evidence that people in ancient China gathered fish after flooding events and transferred them to ponds where they were fed waste from the silkworm industry (Ling 1977, cited in Iwama 1991). Production of fish through these early forms of aquaculture was recognised as a way to reduce the effort required to search for and capture wild fish. In contrast, modern aquaculture is typically an industrialised process whereby a small number of companies on a global scale run and manage large facilities that produce millions of tonnes of fish each year (Naylor & Burke 2005).

A related practice that also involves the captive rearing of fish is stock enhancement. Here, fertilised eggs are hatched and the larvae and fry are reared until they reach a certain stage or size; thereafter, juveniles are released into water systems where the natural population is failing or has been lost. One aim of such releases is to increase the natural or wild biomass of the species concerned. In the case of salmonids, restocking of fish is sometimes used to provide sufficient numbers for sport fishing, but releases are also used to counter the detrimental effects of anthropogenic disruptions, such as dam building, river straightening or effluent pollution that are believed to have contributed to high levels of mortality in natural populations. Marine species, too, have been restocked with the hope of stabilising population recruitment in coastal fisheries (Salvanes 2001). Early attempts at this were made as long ago as the late 19th century in Canada, USA, Russia and Japan, with similar practices tried in Great Britain and Norway in the early 20th century. The motivation for these releases lies in the increasing effort required to harvest wild marine fish, such as the cod (Gadus morhua), haddock (Melanogrammus aeglefinus), pollack (Pollachius pollachius) and plaice (Pleuronectes platessa) (Salvanes 2001). Current changes in climate are now generating shifts in the abundance and distribution of fish species, and these are likely to influence the future of stock enhancement programmes in terms of the species and stocks used (Perry et al 2005).

Over the last four decades we have witnessed a remarkable growth in the fish farming industry, an expansion that is almost certain to continue (Naylor *et al* 2000). Statistics from the Food and Agriculture Organisation of the United Nation (FAO) indicate that aquaculture produced almost 4% of the world's fish (both finfish and shellfish) in the 1970s. Production has since seen a sharp increase and it recently generated *circa* 40% of all the fish humans consume (FAO)



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2002). Indeed, aquaculture is growing more quickly than any other form of food production. With the increasing problems of fish stock collapses and few signs of recovery (Hutchings 2000), aquaculture will become an increasingly important way for us to service the demand for fish protein. Most remaining wild capture fisheries are dependent on subsidies to make their operations financially viable. Expansion of aquaculture practices, therefore, seems inevitable as more and more of the natural fisheries become unworkable and over-fished (FAO 2002). Provision of adequate quantities of fish protein in the future will require that the growth of this industry is appropriately managed. There are concerns, however, that this may not be possible as governments and development agencies may not be capable of keeping up with the rising challenges facing modern aquaculture, such as the stricter codes of practice for decreasing levels of pollution (FAO 2006).

Although a broad range of aquatic organisms are currently produced through aquaculture (from aquatic plants and shellfish to finfish), this report will focus primarily on the culturing of finfish. Several different species are now farmed, but the most common commercially produced fish are the salmonids (consisting mostly of salmon and trout). Improvements in technology have allowed the rapid expansion of salmon farming, and recent years have seen unprecedented increases in the number of individual farms (ICES 2006).

Other species that are commercially farmed include catfish (Ictalurus and Pylodictis spp), carp (Cyprinus carpio), tilapia (Oreochromis spp), sea bass (Sparus aurata), sea (Dicentrarchus labrax), Atlantic halibut bream (Hippoglossus hippoglossus), and more recently cod and tuna (*Thunnus* spp). While representing a smaller section of the aquaculture industry, these other species have presented a number of challenges. Differences in behaviour, physiology, nutritional requirements, disease susceptibility and general robustness require speciesspecific husbandry techniques to be devised. And, as there is an increasing interest in the welfare of farmed fish, finding appropriate solutions to the challenges posed by new emerging species is seen as an important goal.

It can be argued that aquaculture and restocking are important conservation tools - where previously abundant wild populations have become threatened or extinct, we can now rear, maintain and so conserve these populations. Within aquaculture, however, activities such as rearing large numbers of fish in marine cages, or pens, can be detrimental to the local environment and to other organisms living in those environments. For example, intensive farms have been responsible for local pollution caused by excreted waste, and exposure of local wild fauna to antibiotic drugs and other chemicals used to treat the farmed fish. It is, therefore, important to manage the farming situation carefully to minimise any adverse environmental impacts. Other practices associated with aquaculture and stock enhancement are also problematic; for example, it is sometimes necessary to use alien species or strains (including domesticated strains) in certain culture situations. In these cases, the

fish being reared may have origins very different from those of local resident populations. Problems can arise when these alien farmed fish escape and/or interact with wild fish. Potential problems include ecological impacts on the genetic structure of resident populations (Matthews *et al* 2000; Hansen 2002), and the risk of disease transmission (Butler 2002; Heuch *et al* 2005; Krkošek *et al* 2006). Clearly, aquaculture and enhancement activities can have significant environmental impacts and important ramifications for conservation biology (Ford & Myers 2008).

As our ability to rear large numbers of fish has developed, an increasing awareness of the welfare of fish has also grown (Branson 2008). Compared to our understanding of welfare in farmed terrestrial species, fish welfare is in its infancy (FSBI 2002; Lawrence 2008). Yet, recent years have seen a gradual, welfare-driven shift in the techniques and practices used in rearing fish for aquaculture and restocking. Considerable improvements have been made with regard to handling, transport and methods of slaughter (reviewed by Ashley 2007) but further refinements are still required (Huntingford & Kadri 2008). Some of the problems that face fish welfare are determining what fish need and, particularly, establishing which factors adversely affect welfare (Huntingford et al 2006). The diversity of fish species now intensively reared requires the development of species-specific welfare guidelines. Many such guidelines are still missing, especially for the newly emerging species of farmed finfish. We suffer from gaps in our understanding of what constitute desirable stocking densities for different species and how density influences oxygen levels and the build-up of wastes such as carbon dioxide and ammonia (MacIntyre et al 2008; Turnbull et al 2008). We also need to know how normal behaviour is affected by crowding or competitive feeding interactions, and how fish utilise space when confined in a cage or a pen (for example, Ashley 2007). These and related issues are currently being studied and, as consumer interest in the welfare of the fish grows, there is an increasing momentum to find solutions.

Population enhancement through releases of fish also present a number of welfare problems. The potential for overtly aggressive behaviour in released individuals that directly compete with local, wild populations is a concern. Certain feeding practices in hatcheries promote aggression; for instance, when there are only a few food-inlet points these can become a resource that dominant fish aggressively defend. Work has shown that changes in how food is provided can decrease scramble competition and fighting (Andrew *et al* 2002). Aggression in juvenile salmon can also be reduced by adding a number of larger fish into tanks with smaller fish (Adams *et al* 2000). Thus, relatively simple changes to certain hatchery procedures can help to decrease the aggressiveness of fish reared for release.

A different welfare problem is that most fish reared for stock enhancement are ill-equipped behaviourally to survive outside the confines of a hatchery. Inappropriate behaviours, such as poor antipredator responses and naïve

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foraging skills, often result in the vast majority of released fish dying in a few short weeks after release (Olla *et al* 1998; Salvanes & Braithwaite 2006). Current investigations aimed at increasing the survival of released fish are focusing on rearing environments that promote the development of behavioural flexibility and other related traits (Berejikian *et al* 2000, 2005; Braithwaite & Salvanes 2005; Salvanes *et al* 2007).

This review considers both 'welfare' and 'conservation', but as these two terms can be interpreted in a number of ways we need to describe how we define them. We will look at conservation from two perspectives. Firstly, we will consider it as measures taken to increase and protect the numbers of individuals in a threatened population or species. For example, where populations of salmon are threatened through over-fishing, we consider measures taken to increase the numbers of native salmon in that river system as a conservation strategy. Secondly, if the fish have become threatened because of physical changes or disruption to their habitat, then protection and management of the environment and ecosystem could also be considered a conservation strategy. In terms of welfare, we use this term to refer to methods and practices that decrease or minimise the negative effects of culture conditions on fish health, and increase the opportunities for natural behaviour. In the context of fish being used for restocking or escaping fish, we should consider the detrimental effects fish may experience when they find themselves in an environment different from the captive conditions that they have been accustomed to. Similarly, we should also consider the negative effects that the escaped or released fish may have on wild fish or the resident fish that they encounter in the natural environment.

The goal of our review is to highlight issues that we believe are pertinent to conservation and welfare within the context of aquaculture and restocking. For more detailed information on the potential environmental impacts of aquaculture we recommend Iwama (1991) and Naylor and Burke (2005).

The feeding of cultured fish

A nutritious, balanced diet underpins good health and welfare in all animals. Unlike most of the terrestrially farmed animal species that are generally fed vegetarian diets, many of the fish species currently farmed or reared for reintroductions are carnivorous and require feeds that contain fish meal and fish oil. This generates a negative environmental impact because sourcing fish proteins and oils that go into commercially produced fish feed can put further pressure on world fish supplies (Naylor *et al* 1998; Naylor & Burke 2005).

Farming carnivorous fish species generates additional problems because the farmed fish usually require more fishbased material in their diet than they actually produce at harvest. While the fish used to create fishmeal are not typically those used for direct human consumption, carnivorous farmed fish species are often considered to be 'reducers' rather than 'producers' (Naylor & Burke 2005). Such an imbalance is not sustainable, and is a direct example of aquaculture and conservation coming into conflict. Recent improvements in diet technology have reduced the quantities of fishmeal and fish oil in farm feeds; in 1997 approximately 1.9 kg of wild fish were needed to produce 1.0 kg of farmed fish, but in 2001 only 1.3 kg of wild fish were required (Naylor & Burke 2005). While this decreasing ratio is encouraging, the advantages of such a reduction can be outweighed by rapid increases in the total number of fish now being farmed. Many of the fish proteins and oils are now being replaced with plant-based products, but from a welfare perspective, the use of plant protein and oils in a carnivorous fish diet is not natural. The effects of new feeds must be carefully assessed, not just in terms of growth rate of the farmed fish, but also in terms of the effect they have on appetite and hunger (Torstensen *et al* 2008).

Of more concern is the fact that several of the new, emerging farmed species of finfish have even higher demands for fish protein in their diet. Tuna, for example, which in the wild feed on mackerel (Scomber scombrus), anchovies (Engraulis australis) and sardines (Sardinops sagax), need to be fed raw diets or diets that are rich in protein and oils (Svane & Barnett 2008). Dietary requirements should be an integral part of the decision about which emerging aquaculture species are to be selected. Furthermore, as wild fish numbers continue to decline and they become harder to obtain, it will soon be too expensive to produce food for the captive fish. Solutions to this problem will require innovative approaches and a willingness by both private-sector businesses and governments to support more ecologically integrated practices (Costa-Pierce 2002). Current research is focusing on ways to manufacture more vegetable-based feeds or feeds based on other sources of protein, such as poultry. In addition, more lowertrophic-level finfish species should be considered for farming in the future (Naylor & Burke 2005).

Cannibalism (intra-specific predation) is another problem associated with rearing carnivorous fish. It is of concern because it increases costs of juvenile production, and it potentially represents a welfare problem (Baras & Jobling 2002; Forbes 2007), the main welfare concern being the fear and harassment of fish living in a tank that contains individuals that have become cannibalistic. Certain species seem to be more prone to cannibalism than others (eg Hseu et al 2007). There are suggestions that specific stages in life may trigger the behaviour; in cod, for example, cannibalistic behaviour is believed to increase around the time of metamorphosis as the fish switch to an adult lifestyle (Forbes 2007). The risk of cannibalism can be decreased if older fish are stocked at higher densities (Baras & Jobling 2002), and also if fish are graded into similar-sized groups as happens with farmed salmon and trout (Leitritz & Cronklin Lewis 1980). The mechanisms that underpin cannibalistic behaviour remain poorly understood, and on welfare grounds alone, this should be a research priority.

Not all farmed fish are carnivorous. For example, tilapia can be fed a diet that is less rich in protein. Tilapia culture has consequently seen a considerable expansion, and it has

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become a popular fish for many small-scale aquaculture projects across the world (Teichert-Coddington & Green 1993). The culture system uses freshwater and is completely enclosed. The fact that the fish feed on detritus and algae makes them an excellent candidate for small subsistence farmers. In some countries, small-scale tilapia culture is run alongside small-scale pig and chicken farming, with the waste from these animals being used to fertilise the tilapia ponds to promote algal growth.

The choices farmers make about which species to farm are led ultimately by consumer demand. If we want newly emerging aquaculture species to include fish that are from lower trophic levels, we should find ways to encourage consumers to buy and eat fish that naturally have a more herbivorous lifestyle.

How aquaculture and fish rearing affect the local environment

Problems with waste

With improving technology there has been the opportunity to expand the size and number of sites used for fish farming, leading to more intensive farming practices. This expansion has been accompanied by an increase in the environmental impact of fish farming through the increased use of artificial feeds and the use of chemicals (Ervik et al 1997; Hansen et al 2001; Stigebrandt et al 2004; Cabello 2006). Pollution from excess feed and fish faeces has led in the past to a high production of sediments over large areas surrounding fish farms (reviewed in Iwama 1991), and the resulting carbon flux to the sea-bed can be several orders of magnitude higher than natural fluxes (Hall et al 1990). Such high loads of organic material create anaerobic sediments containing hydrogen sulphide (Hansen et al 2001), and these environments become rich in microfauna, such as sulphate-reducing bacteria (Holmer & Christensen 1992). These changes also underlie shifts in the benthic, or bottom-dwelling, animal communities found under the sea cages. Typically, these contain more species that can tolerate low-oxygen environments such as polychaete worms (Hansen et al 2001). Other effects include a decrease in sea grass production and cover (Ruiz et al 2001). Larger wild fish also respond to changes in the waters around fish farms; wild, adult cod prefer to avoid waters from both salmon and cod fish farms. Interestingly, however, escaped farmed cod do not show such avoidance responses and appear to stay close by the farms that they escape from (Sæther et al 2007).

The destruction of local habitats, and the forced changes to the animal and plant communities in the areas adjacent to fish farms, became a key problem as aquaculture intensified (Iwama 1991). It soon became obvious that site selection for the farms was very important, with shallow or sheltered areas being unsuitable as the rate of sedimentation of waste particulate matter is too high. Fish maintained in pens or cages where there is a good flow of water perform better, as the suspended wastes are dispersed more readily. Water flow also improves the supply of oxygen to the fish in the pens and to biota in the surrounding environment (Iwama 1991). Other practices have also led to improvements in the quality of the sediments underneath and near the farms. Devising ways to reduce feed waste have helped in such cases. For instance, video-monitoring the fish allows the onset of satiation to be observed and indicates how much food should be offered. Other approaches involve the use of demand feeders, and feed retrieval systems that prevent uneaten food from settling outside the pens (Alänära 1996; Fernö et al 2006). Furthermore, changes in feed composition have helped; nutrient discharge around rainbow trout (Oncorhynchus mykiss) pens was much reduced when plantbased feeds were used instead of those rich in fish meal and fish oil (Papatryphon et al 2004). Other attempts in freshwater systems have included investigating the effects of lower phosphorous diets to further decrease the environmental impact (Oliva-Teles & Pimentel-Rodrigues 2004).

The expansion of aquaculture also affects the size of natural nursery environments that are available for wild coastal fish populations. Fish farms are normally situated in the same coastal areas where early lifestages of local fish populations live. For example, juvenile cod in Norwegian fjords settle into well-oxygenated, near-shore habitats where cobble and kelp serve as shelter, and provide habitat for their prey (Nordeide & Salvanes 1991). These sites, however, are typically the locations also chosen for fish farms. As we have reported above, loading of organic matter from fish farm cages alters the surrounding environment, potentially degrading habitats that provide important nursery environments. Shelter opportunities become restricted when sediments accumulate over stones and gravel, and invertebrate and fish numbers decrease. Tropical regions have also experienced the devastating effects of clearing mangroves to prepare areas for fish and shrimp culture. Attempts to quantify the effects that the loss and clearance of mangrove areas has on juvenile lifestages are reviewed by Iwama (1991). To our knowledge, this type of conflict between aquaculture and areas of suitable nursery environment for local fish populations in more temperate environments is yet to be evaluated; it would seem highly probable that a conflict will exist.

Providing fish with good water quality and good levels of flow, whether in enclosed freshwater systems or in larger flow-through cages, is also a welfare issue for farmed fish. Better water quality with efficient removal of waste promotes a healthier environment. Care needs to be taken when cages are placed in regions with natural flow, such as in tidal areas, because the flowing water can distort the fish cages. Currents that squeeze and pull on cages can reduce the volume of the cage that is available for the fish to use which, in effect, increases the density of the fish within the cage. Cage deformation can also result in skin abrasions if the fish are pushed or forced against the mesh cage walls by strong tidal currents (Turnbull et al 2008). Underwater cameras that allow the cage shape to be monitored, and acoustic measures that indicate where in the cage the fish are swimming, can be used to monitor these types of hazard. In enclosed, land-based fish farms where freshwater species are produced, decisions on the appropriate flow rate are also

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The costs of keeping fish healthy

Fish that are stressed do not grow well, so it makes sense for the farmer to care about and pay attention to the health of their fish. Increased prevalence of disease, even in relatively low stress situations, is a natural consequence of high-density living conditions. Trying to keep fish free from disease is an important aim of fish welfare. Sick or diseased fish can show clinical signs of illness; for example, swimming behaviour can become altered, but changes associated with illness are often difficult to detect. When there is an acute disease, fish can become moribund and the welfare of the fish in this state is a clear problem (Wall 2008). Although occasionally logistically difficult, it is desirable to remove sick or dead fish from tanks or pens as swiftly as possible. The sick fish represent an unwanted source of infection, and they can create problems for water quality as carcases begin to break down, which further compromises the welfare of fish confined within the same tank or pen (Wall 2008). Furthermore, many of the routine handling and husbandry practices involved in aquaculture often compromise the efficacy of the fish immune system because they are considered to be stressful for the fish (Barton & Iwama 1991; Cabello 2004 cited in Cabello 2006).

As stress has been shown to be immunosuppressive and because it can impair the ability of fish to fight off bacterial infections, the aquaculture industry has used prophylactic antibiotics (Cabello 2006). For many years this seemed to be the only way to maintain fish health and welfare. The use of antibiotic and other antimicrobial drugs within the aquaculture industry has, however, posed serious threats to local habitats. Unrestricted use of antibiotics has now resulted in various antibiotic-resistant bacteria in the sediments and the water column surrounding the farms (Chelossi et al 2003). More alarmingly, there is growing evidence that genetic elements that confer antibiotic resistance are able to transfer between organisms and these genetic sequences are now appearing in other niches including human, and other animal disease, organisms (Angulo et al 2004; Sørum 2006). In the long term, this may have a negative impact on the farming industry itself, as diseases with increasingly resistant pathogens are likely to evolve. Such an 'arms-race' can generate pathogens that not only affect fish, but that also threaten the health of humans and other animals that consume products of aquaculture (eg Holmstrøm et al 2003; Duran & Marshall 2005; Cabello 2006).

In developed countries, the use of antibiotics is now heavily regulated and this has led to a substantial decrease in their use (Markestad & Grave 1997; Angulo *et al* 2004). This decrease has been assisted by the development of a number of fish vaccines (Markestad & Grave 1997; Weber 2003). Several developing countries still continue to use a range of antibiotics to control the outbreak or spread of diseases on

fish farms. There is growing concern that the largely unregulated use of antibiotics in countries experiencing expansions in their aquaculture industry (such as China) may encourage the emergence of new strains of antibioticresistant bacteria. Research and development into more effective vaccines and ways that these could be provided cheaply, should be a priority for the industry.

Fish farms are frequently blamed for the emergence of new diseases in sympatric wild fish populations; however, the extent to which fish farms are to blame has been the topic of considerable debate. Pinning down the precise threat that aquaculture brings to coastal habitats and ecosystems has proved to be difficult (McVicar 1997, 2004; Cubbitt et al 2006; Ford & Myers 2008). This may, in part, reflect the fact that different populations vary in their susceptibility to different types of infections based on what they, or their ancestors, have been exposed to in the past. Most fish diseases are likely to originate in wild populations, and wild fish may therefore have natural defences to cope with such diseases, however, if a novel disease is accidentally introduced into an area then 'naïve' local populations may struggle to cope with it. Cubbitt and colleagues (2006) suggest that restocking programmes represent a bigger disease threat than aquaculture. With one escaped farmed fish getting into the environment for every two-million stock enhancement fish that are intentionally released, any pathogen or disease present in hatchery-reared stock enhancement fish would seem more likely to spread to wild fish (but see Ford & Myers 2008 who argue that there is a direct effect of aquaculture on the decline of wild populations).

Indeed, it is known that large releases of hatchery-reared fish were the cause of the devastating spread of the monogenean parasite, Gyrodactylus salaris, that effectively wiped out wild salmon from several northern Norwegian rivers (Johnsen & Jensen 1991). But does a fish need to be swimming outside the confines of a sea cage or pen to be a disease threat? The answer, according to Krkošek and colleagues (2006), appears to be no. They suggest that sea lice (Lepeophtheir salmonis) infestations in wild pink salmon (Oncorhynchus gorbuscha) and chum salmon (Oncorhynchus keta) may be affected by the presence of fish farms. Normally, the transmission of lice between adult and juvenile fish is prevented because the migratory lifestyle segregates fish of different ages. Sea cages and pens located in areas wild juvenile fish move into may, however, break down this spatial barrier, and Krkošek et al (2006) propose that fish farms could undermine the normal spatial separation of different life stages of salmon. If true, this finding has important ramifications for salmon and other aquaculture species that incorporate some form of migration into their life history; species such as sea bass and cod, for example, could be affected by increasing risk of disease transmission between juvenile wild fish and captive adult farm fish.

Between 1992–1996 and 2001–2003, a different disease devastated the Atlantic salmon aquaculture industry in British Columbia. The disease was infectious haematopoietic necrosis virus (IHNv). It had previously been well documented in the native wild stocks of Pacific salmon, but

something caused the virus to become infective towards farmed non-native Atlantic salmon and this resulted in an average of 40–70% mortality in these fish (Karreman 2006). The transfer of this virus was believed to have occurred as infected, migrating, wild, native salmon returned and moved into estuaries passing cages containing the non-native Atlantic salmon.

Clearly, both restocking practices and the positioning of sea cages along migratory routes can effectively increase disease transmission between reared/farmed and wild fish, and vice versa. It remains to be determined how best to address these greater risks of infection, but perhaps treating farmed fish for infections immediately prior to the start of the juvenile migration phase may be beneficial, and decreasing the numbers of fish that are released for stock enhancement might also go some way to decreasing the risk of infections spreading into wild populations. Similarly, being vigilant for early signs of infection during periods when there may be greater susceptibility to disease transmission, such as during migratory phases, could also be beneficial. Setting up marine protected areas associated with known migration routes, and ensuring that sea cages are placed well away from such areas and away from prevailing water currents that may assist pathogen or parasite movements, should help to limit disease transmission between wild and farmed fish.

What effects do alien fish populations and species have on local populations?

In the following section, we take a more detailed look at the consequences of either accidental escapes from farms, or the intentional release of millions of fish through stock enhancement.

Wild fish populations are genetically adapted to their local environment, whereas domesticated fish such as Atlantic salmon and cod are selectively bred to maximise biomass production in captivity. Farmed fish are also from founder populations that often have a different geographical origin compared to the wild populations surrounding fish farms or hatcheries. For example, Norwegian farm strains are now used in all salmon farming countries, and Norwegian farm strains of cod are currently being developed (McGinnity *et al* 2003; Dahle *et al* 2006; Skåla *et al* 2006). High growth rate is a typical trait that is selected for in farmed salmon (Hindar *et al* 2006). This means that domesticated strains of salmon will always differ from wild fish.

Domestication has tended to favour aggressive behaviour in Atlantic salmon, and escapees therefore have traits that may allow them to out-compete fish from local populations of the same species (Huntingford 2004). In some cases, this is believed to make escapes of farmed salmon a threat to wild populations, and this raises questions concerning the wellbeing of wild fish that interact with escaped fish. For example, seventh-generation farmed juvenile Atlantic salmon from Norwegian rivers were found to grow faster and were more aggressive than wild fish, and the farmed fish also dominated wild fish from the same rivers in pairwise contests when competing for food and territories (Einum & Fleming 1997; Fleming & Einum 1997). Mature farmed Atlantic salmon can also spawn successfully and hybridise with wild fish in Irish and Norwegian rivers (Lura & Sægrov1991; Crozier 1993; Clifford et al 1998). As much as 30–80% of Norwegian river populations may be escapees (Fiske & Lund 1999; Fiske et al 2006). Offspring from escapees and hybrids are not always as robust as wild juveniles; interaction with farmed escapees weakens fitness and disrupts local adaptation. These detrimental effects can create problems in the gene pool of the wild populations (McGinnity et al 2003). Immunity can change; the immune response gene, MHC I, was observed to decrease its variability in a river population of trout after aquaculture activities started (Coughlan et al 2006). The authors suggested that local salmonid farms were indirectly responsible for this reduced immune function, with infections from the farmed fish spreading through and reducing the frequency of certain genotypes from the trout populations.

Farmed salmon smolts often have higher infection rates of sea lice than hybrids and wild salmon (Glover & Skåla 2006). Escapees can be host to parasites that would not normally be found in local wild fish populations. After the fish escape, their interactions and overlap with local species can promote the spread of these parasites in individuals that have little or no resistance to infection (Dunn 2009). Simulation models suggest that 20% of farmed salmon escaping would be sufficient to prevent the recovery of a natural, wild population (Naylor *et al* 2005; Hindar *et al* 2006).

The loss of fish from farms represents a considerable economic cost to the aquaculture industry, so it is not surprising that steps are taken to minimise escapes. A growing concern for newly emerging finfish species is that some are more effective at escaping than others. Cod, for example, tend to manipulate objects in their mouths and this has led to a number of escapes where the fish have literally nibbled through the nets of the sea pen (Moe et al 2007). Moe and colleagues (2007) suggest cod are, in fact, much more proficient at this than salmon. However, escaped farmed cod may be easier to recapture than escaped farmed salmon as they remain close to the net area even after escaping (Uglem et al 2008). The development of pens that make it harder for cod to escape, in combination with an efficient recapture programme, might lessen the impact of farmed cod on wild populations.

Not all species of farmed fish pose the same level of threat in all locations. The study by Cubbitt and colleagues (2006) also investigated the success of Atlantic salmon escapees in West Coast Canada, and the capacity for these farmed fish to hybridise with local salmonid species. Their study found no evidence of hybridisation between Atlantic salmon and Pacific salmonid species in the Pacific Northwest. The authors also reported extensive laboratory studies that failed to create viable offspring when Atlantic salmon were crossed with pink, chum or coho salmon (Chevassus 1979; Longinova & Krasnoperova 1982; Gray *et al* 1993). Furthermore, escaped Atlantic salmon are unable to compete

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successfully with Pacific salmon. There appears to be only one report of Atlantic salmon establishing a self-sustaining population outside the normal range of this species and this was found in New Zealand (Lever 1996). Thus, in Northwest Canada, escapes of farmed Atlantic salmon do not represent much of a threat to native Pacific salmon populations. A recent meta-analysis assessing the global impact of farmed fish on wild populations, however, paints a bleaker picture suggesting that in some cases and in certain locations, wild salmon abundance has declined by more than 50% as a result of salmon farming (Ford & Myers 2008).

What consideration is given to the genetic background of the fish used in restocking?

Similar concerns arise over the fish reared and released for stock enhancement. Populations distributed over a wide range of environments may form distinct sub-populations that vary in life-history traits (Law 2000). Wild fish populations of both Atlantic salmon and cod, for example, show these kinds of genetic differences across geographic regions (eg Taylor 1991; Dahle *et al* 2006), and these are relevant for stock enhancement programmes. The biomass production of sub-populations depends largely on factors such as growth and mortality rates, age and size at maturation, and fecundity. These life-history traits all influence fitness, and sub-populations should therefore adapt to local selection regimes (Sutherland 1996; Carrol & Corneli 1999; Law 2000). Populations from different geographical regions will differ in these traits.

Most organisms are actually capable of growing much faster than they do in nature (Calow 1982). One reason is that local temperatures may limit expressed growth (Jobling 2002). Thus, different populations of fish can have locally adapted growth patterns that reflect the average temperature fluctuations within their distribution. Along a latitudinal gradient there will be changes in ambient temperature as well as other environmental variables. Growth is generally more constrained at higher latitudes owing to a shorter growing season and lower temperatures. To counteract the negative effect of the environment on growth, high-latitude populations can evolve adaptations to maximise growth, ie countergradient selection (Levins 1969; Hutchings & Morris 1985; Conover & Present 1990; Conover & Schultz 1995; Arendt 1997; Foster & Endler 1999; Jobling 2002). If offspring of fish from areas with environmental constraints on growth are released into wild populations in areas with more profitable environments, these released fish may out-compete and replace wild fish rather than enhance the population.

In the Northern hemisphere, species that experience counter-gradient selection on growth show higher growth potential in high-latitude populations compared to their southern conspecifics (Salvanes *et al* 2004). One-year-old wild-caught coastal cod caught at 70°N were smaller, grew more slowly, weighed less, and had a lower body condition factor than southern cod from 60°N during a sampling period between June and February. In contrast, the northern cod showed both a higher growth potential and an increase in body condition factor when northern and southern cod

were housed together in a 'common-garden' experiment. The rapid growth of the northern cod was achieved by higher success in food competition when given a restricted amount of food (Salvanes *et al* 2004). Higher growth potential could be achieved by higher food consumption through more active feeding behaviour and higher competitive ability. The role of restocking as a way to restore threatened and endangered populations therefore requires conservation of the genetic diversity of the wild populations. Swapping brood stock across geographical regions should therefore be avoided.

Concern about hybridisation with wild fish is an issue for restocking programmes. For example, use of non-local fish for stock enhancement runs the risk that local adaptation may be disrupted if released fish breed with local populations, and this may compromise long-term survival. Careful selection of brood stock is therefore essential if restocking is to have a positive effect. Failure to use appropriate broodstock may harm the welfare of the released fish, if these fish are simply unable to perform appropriately in the new environment. Selecting broodstock to produce offspring for reintroductions is therefore a highly complex decision.

Non-native fish may well do more harm than good, and may also cause problems for any remaining wild fish in the area. To promote survival in a specific habitat, fish released for restocking should, where possible, be of local origin. Furthermore, recent evidence has shown that just two generations in captivity can negatively influence inclusive fitness of broodstock, suggesting that where possible wild-caught, local broodstock should be used for stock enhancement programmes (Araki *et al* 2007).

Does the captive rearing environment compromise the welfare of fish reared for restocking?

Fish reared for restocking experience captive environments that do little to prepare them for the trauma of life outside the hatchery. This affects the welfare of the released fish. Inside the hatchery, fish are housed in predator-free conventional tank environments or semi-natural ponds where food is plentiful and the environment is safe. Although releasing practices vary, large numbers of naïve fish are often released at high densities into streams or the coastal environment. Most of these fish die (Olla *et al* 1998).

In order for released fish to survive, they must possess basic behavioural skills that allow them to find suitable food and shelter, and that provide them with other anti-predator strategies. These fish must learn to capture live prey, a task that many hatchery fish fail to master, and to feed efficiently (eg Ersbak & Haase 1983; Ellis *et al* 2002). It has been reported that some hatchery fish use more energy and have higher feeding activity to capture wild prey when compared with wild individuals (Steingrund & Fernø 1997). Higher feeding activity increases the rate of encountering predators and thus increases predation risk. Predator-naïve cod are more prone to predators than experienced cod (Nødtvedt *et al* 1999). Empirical field data have demonstrated the high rates of mortality experienced by most released hatchery fish (reviews in Olla *et al* 1998; Weber & Fausch 2003). Again, this raises a number of ethical and welfare-related issues. Should we release fish that are so behaviourally illequipped that they will have a high mortality rate?

Although growing and developing in a conventional hatchery does little to prepare fish for the transition to a variable natural environment, it may be possible to rear more behaviourally competent fish. For example, juvenile cod exposed to enrichment in their rearing tanks showed greater behavioural flexibility than cod reared in conventional, barren tanks (Braithwaite & Salvanes 2005; Salvanes & Braithwaite 2005; Salvanes *et al* 2007). Enriched-reared cod improved their ability to consume live prey in the presence of foraging tutors (Strand 2007), and were better at responding appropriately to predation threats (Langård 2007). Adding enrichment into the tanks of fish reared for restocking therefore has the potential to improve survival, and may also improve the welfare of fish because there is less stress and trauma involved in transitioning to a new environment.

Finally, releasing fish into habitats that have already been shown to be inadequate for wild fish is unlikely to result in increased population size. If a river or coastline has been modified in a way that threatens the wild population, then releasing more fish will probably achieve little. Therefore, it is important to consider measures, such as habitat reconstruction, alongside restocking activities to improve the success of enhancements approaches.

Does the captive rearing environment compromise the welfare of fish reared for food?

There are ongoing debates about what it may mean for fish to suffer, and what types of emotional capacities fish have (Braithwaite & Boulcott 2007; Rose 2007), but beyond these debates there is clearly a growing acceptance that fish can experience pain and some form of suffering (Chandroo *et al* 2004). Recent advances in our understanding of fish stress physiology and fish cognition have emphasised the need to create appropriate guidelines and codes of practice to promote fish welfare (Huntingford & Kadri 2008). The welfare of farmed fish can be difficult to quantify, but several measures have focused on the functioning of the fish. This function-based approach uses assessments of physical condition and behaviour to indicate welfare status (Huntingford & Kadri 2008).

The fish farm is an inherently stressful place. Fish are kept at unnaturally high densities where water quality and access to space are often compromised. Feeding can lead to scramble competition when several fish chase after a limited number of food items; this can generate increased aggression which may lead to injury (reviewed in Ashley 2007). Skeletal deformities and abnormalities in tissues and organs are also present in farmed fish; similar pathologies arise in wild fish too, but such deformities typically persist for longer in farmed fish (Branson & Turnbull 2008). Compared to wild fish, farmed fish are also handled more frequently, something that triggers a physiological stress response in most fish (Ashley 2007). Handling can be necessary for sizegrading or when fish need to be transported to a new site. And, finally, once the fish have grown to the desired size they are collected for slaughter (Robb 2008).

The previous decade has seen increased interest in the welfare of farmed fish, and considerable research aimed at improving fish welfare. Physiological and behavioural assessments of stress responses have been instrumental in allowing us to devise better handling techniques that reduce the amount of time fish are actually out of water (reviewed in Ashley 2007). There have also been improvements in slaughter methods and better feeding methods that lower levels of competition (Ashley 2007; Branson 2008). Research is also currently investigating ways of reducing the numbers of deformed or abnormal fish generated in aquaculture (Branson & Turnbull 2008). Thus, while the captive environment can compromise the welfare of fish, considerable effort is now being directed at reducing these negative effects (Branson 2008). There is still much to be improved. Key areas that should be addressed are species-specific slaughter methods with appropriate stunning techniques (Ashley 2007), and more refined methods for determining appropriate stocking densities (Turnbull et al 2008).

Animal welfare implications and conclusion

Improvements in fish husbandry skills, largely driven by the aquaculture industry, now allow us to captively rear enormous numbers of fish from egg stages through to adults. With the expansion of the aquaculture industry, an interest in the welfare of fish has developed. Closely linked to this is a growing awareness of the negative effects that farmed fish can have on local environments and the animals that inhabit these. Thus, welfare and conservation are clearly linked within the context of aquaculture and stock enhancement. Growing awareness of animal welfare is encouraging us to reconsider some of the methods used to rear fish, and the need to conserve and protect natural environments underpins several recent refinements in aquaculture practices. As harvesting wild fish becomes less economically viable, fish farming will continue to expand. The future of sustainable aquaculture and successful stock enhancement will lie in our ability to understand and maintain healthy fish populations both in and outside captivity.

Acknowledgements

We thank Shannon Balfry, David Fraser, Sunil Kadri, Fiona Mathews and Dan Weary for their comments and discussion.

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