Politics and pride: Maintaining genetic novelty may be detrimental for the conservation of Formosa landlocked salmon *Oncorhynchus formosanus*

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Abstract

1. Populations of conservation concern are often rare, restricted in range, and isolated from other populations. This can manifest in low genetic diversity, which reduces the ability of a population to respond to changes in the environment, and in higher levels of inbreeding, which reduce individual fitness. Isolated populations, however, often harbour genetic and phenotypic novelty, which can elicit a strong community sentiment to maintain these populations.

2. Genetic rescue – the introduction of genetic variation to improve fitness – offers potential benefits for isolated and threatened populations, but has associated risks, including a perceived loss in identity if that population is geographically, genetically, and culturally significant. Here, the potential benefits and risks of genetic rescue for isolated freshwater populations are discussed, using the Formosa salmon as an exemplar.

3. Formosa landlocked salmon, a member of the masu salmon complex (*Oncorhynchus masou* sensu lato), is the southernmost naturally distributed salmonid in the world, occupying a single stream at high elevation in Taiwan. Listed as Critically Endangered, it exhibits continuing low abundance (<5000 individuals). Although Formosa salmon can be genetically distinguished from other masu salmon, its genetic variation is extremely low and genetic factors may now critically affect fitness.

4. There appears to be clear merit for the genetic rescue of Formosa salmon, and test crosses involving other landlocked masu salmon are urgently required. If these test crosses yield individuals of high fitness, guidelines for introductions into the wild are provided. In addition, subpopulations above and below artificial instream barriers to movement require connection via the direct exchange of individuals to minimize any further losses of genetic variation. Insurance populations with independent risk probabilities to the existing population should also be constructed, with continuing connectivity among populations through the direct exchange of individuals.

**KEYWORDS**

agriculture, fish, genetics, impoundment, pollution, rare species, stream
Populations of conservation concern often exhibit a suite of problems: low abundance, restricted range, loss or degradation of essential habitat, and perturbation from non-native species. A common consequence of such factors is the loss of genetic variation in a population, either through reduced abundance (with increased genetic drift and inbreeding) or through the loss of connectivity with other populations (with reduced gene flow) (Frankham, 2010a). Genetic drift in small populations can decrease allelic diversity, reducing the ability of a population to respond to changes in the environment (Frankham, 2010a), while also potentially increasing the frequency of slightly deleterious alleles (Hedrick & Fredrickson, 2010). Within smaller populations, increased levels of inbreeding have the ability to expose more deleterious alleles in the homozygous state, reducing individual fitness through inbreeding depression (Frankham, 2010a). Loss and fragmentation of habitat inhibits the ability of gene flow to elevate allelic diversity and reduce levels of inbreeding.

Although there are strategies to overcome the proximate causes of species decline, they will not necessarily recover the genetic diversity of a population. Captive-bred individuals can be released, range contraction can be remedied through reintroductions and translocations, habitat can be restored, and invasive species controlled. These actions may seek to increase the abundance of a threatened population, or maintain its presence and minimize any future loss of genetic diversity, but they cannot reverse the loss of genetic diversity already experienced except in circumstances where habitat restoration improves the connectivity between genetically distinct populations (Proft, Jones, Johnson, & Burridge, 2018). Furthermore, even if the proximate factors for the decline of a species have been rectified, the decline in genetic diversity and individual fitness already experienced may now inhibit population recovery in its own right. Only the introduction of alleles from genetically distinct populations or species can increase genetic diversity in an imperilled population. This can also increase individual fitness by heterosis, a process termed ‘genetic rescue’ in conservation biology (Frankham, 2015; Hogg, Forbes, Steele, & Luikart, 2006; Johnson et al., 2010; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015). Similarly, under situations where the proximate causes of population decline cannot be removed (e.g. land clearing for human habitation), increasing genetic diversity represents a potential mechanism to offset their continued impact. Perhaps the most high-profile success story involves the Florida panther, considered by some to be a regionally distinct subspecies of Puma concolor, that was recovered via the introduction of novel alleles from a Texas population (Johnson et al., 2010).

An argument used against the introduction of genetic variation into an imperilled population is the potential for outbreeding depression: a reduction in fitness accompanying the crossing of distinct lineages (Edmands, 2007). However, recent empirical studies and reviews indicate that the risks associated with outbreeding depression have been exaggerated (Fitzpatrick et al., 2016; Fitzpatrick, Gerberich, Kronenberger, Angeloni, & Funk, 2015; Frankham et al., 2011; Kronenberger et al., 2017; Weeks et al., 2011), and are only significant when the lineages involved have fixed chromosomal differences (with potentially infertile offspring), histories of long isolation, or inhabit substantially different environments (Frankham et al., 2011; Weeks et al., 2011). In some instances, a short-term decline in fitness can be expected as divergent alleles are combined (Hogg et al., 2006), but natural or artificial selection in subsequent generations (assuming that they are viable) can remove less fit genotypes, leaving those that are minimally as fit as the starting population, if not fitter (Carney, Gardner, & Rieseberg, 2000; Edmands, Feaman, Harrison, & Timmerman, 2005; Erickson, Fenster, & Husband, 2006; Frankham et al., 2011; Weeks et al., 2011). In Florida panthers, for example, some introduced alleles were retained and probably explain the elevated fitness observed (Johnson et al., 2010). A decline in fitness in the first generation following the introduction of new alleles is not a signal to stop the intervention.

Although genetic rescue will increase the genetic diversity of a population, it will also reduce its genetic distinctiveness, and there has been a tendency for conservation genetic studies to advocate the preservation of genetically distinct populations (Weeks, Stoklosa, & Hoffmann, 2016). The genetic distinction of populations indicates that they are probably demographically independent, and therefore at greater risk of decline from local pressures given low levels of immigration (Carvalho & Hauser, 1995). Genetically distinct populations could also be locally adapted (Moritz, 1994). Therefore, the identification of genetically distinct populations can direct monitoring and management actions at the most appropriate spatial scales to achieve regional abundance targets and maintain any locally adaptive genetic variation. However, the identification of genetically distinct populations is often used to advocate the maintenance of their genetic novelty per se, even when there is no evidence for local adaptation, or when the genetic distinctiveness has resulted from the processes responsible for the decline of the population, such as reductions in abundance and range fragmentation (Weeks et al., 2016). Given that populations of conservation concern are typically narrowly distributed and often peripheral (e.g. ‘southernmost’), they are also often subjects of pride in local human communities, exemplified by their portrayal on postage stamps, currency, and emblems, and by the well-publicized release of captive-bred individuals by politicians. Therefore, there is also strong community pressure to maintain genetic distinctiveness despite the apparent inability of a population to perform well in its present environment (assuming that problems with its environment cannot be otherwise remedied).

Despite pressures to maintain the genetic distinctiveness of populations of conservation concern, there is now compelling evidence for genetic rescue as a management action (Frankham, 2015; Whiteley et al., 2015). Here I discuss the merit for genetic rescue in the Taiwanese Formosa salmon. This species represents an exemplar for many narrowly distributed and regionally significant freshwater taxa of conservation concern, and hence the points discussed are broadly applicable.
The Formosa landlocked (non-marine-migratory) salmon, like many imperilled freshwater taxa, is narrowly distributed. It lives only in a 7-km stretch of Chichiawan Stream, a high-elevation (1700 m a.s.l.) tributary of the Tachia River in central Taiwan (Healey, Kline, & Tsai, 2001). It is the southernmost naturally occurring salmonid in the world. It is recognized as a member of the cherry or ‘masu’ salmon complex (Oncorhynchus masou, sensu lato), which is otherwise distributed in the Japanese Archipelago, the Korean Peninsula, and several Russian drainages around the Sea of Okhotsk (Morita, 2018) (Figure 1a). Therefore, the Formosa salmon is more than 1000 km distant from its nearest relative. Although genetically distinguishable at amplified fragment length polymorphism (AFLP) markers (Gwo, Hsu, Lin, & Chou, 2008; Hsu et al., 2010), genetic divergence from other masu species appears to be limited, and for mitochondrial cytochrome b sequences only a single haplotype is observed for Formosa salmon, and this is also represented in Japanese masu salmon (Iwatsuki, Ineno, Tanaka, & Tanahara, in press). It is hypothesized that Formosa salmon have been genetically isolated since the Last Glacial Maximum (Gwo et al., 2008; Hsu et al., 2015), which seems reasonable given that the temperatures of lowland Taiwanese streams at present exceed tolerances for salmonids (17°C) and no anadromous individuals have ever been encountered nearby. The taxonomy of Formosa salmon has long been contentious, either recognized as a full species (Oncorhynchus formosanus) or as a subspecies of masu salmon (O. m. formosanus) (Ho & Gwo, in press). In the most recent assessment, the morphological distinction of Formosa salmon from other masu was confirmed based on fewer vertebrae, anal fin rays, and pectoral fin rays (Chang & Gwo, 2009). Herein, the population in Chichiawan Stream will simply be referred to as ‘Formosa salmon’, and the focus of this article is on the conservation of this population, regardless of its taxonomic rank.

The abundance and range of Formosa salmon has declined since the 1960s (Figure 1b), coincident with the development of agriculture in the catchment (Tsao et al., 1998) and the construction of erosion control ‘check dams’ in the 1970s (Wang, Kuo, & Chang, 2013) that in some cases exceed 10 m in height. The abundance of Formosa salmon has been estimated using snorkelling surveys rather than with

**FIGURE 1** (a) Distribution of spawning rivers of masu salmon (Oncorhynchus masou sensu lato) and nearshore marine distribution of the anadromous form (blue), derived from Morita (2018). (b) Past (Tsao, Lin, Behnke, & Bergersen, 1998) and present distribution of Formosa landlocked salmon, including the location of instream barriers, based on Chung et al. (2008), Hsu, Takata, Onozato, and Gwo (2015), and Chang et al. (2017). (c) Aerial image illustrating the extent of land clearing adjacent to Chichiawan Stream. (d) Recently decommissioned check dam. (e) Exemplar of the cultural recognition of Formosa salmon, featured on the highest denomination Taiwanese banknote.
any form of capture-mark-recapture technique. Annual abundance averaged 1323 individuals from 1987 to 2004 (Tzeng, 2004), and between 1000 and 5500 since 2005, but was as low as 200 in 1984 (Lin & Chang, 2016). The presence of sex-ratio bias towards females (Hsu, Chen, & Gwo, 2016) lowers the effective size of the population \( N_e \) through unequal contributions of individuals to future generations (Waples, 2002). Formosa salmon remains threatened by habitat deterioration from agriculture and development within the headwaters of the Tachia system (Figure 1c), and range fragmentation from check dams (Healey et al., 2001), although there has been a recent removal of some dams (Figure 1d; Chang et al., 2017; Lin & Chang, 2016; Wang et al., 2013). Formosa salmon is listed by the International Union for the Conservation of Nature (IUCN) as Critically Endangered (Kottelat, 1996), and is a subject of national pride (Figure 1e).

The Formosa salmon exhibits lower genetic diversity than other masu salmon (Hsu, Wang, et al., 2010; Tzeng, Lin, Lin, Wang, & Wang, 2006). A recent survey found no mitochondrial DNA polymorphism among 50 Formosa salmon, 18 out of 44 individuals lacked any microsatellite polymorphism, and allelic diversity and heterozygosity were otherwise by far the lowest of the masu salmon populations surveyed (S. Yamamoto, pers. comm., November 2017). This mirrors an earlier assessment that revealed no polymorphism at mitochondrial DNA and all but one microsatellite locus (Hsu et al., 2015). Although a naturally small population size could be responsible for observations of low genetic diversity (Vincenzi, Crivelli, Jesensek, & De Leo, 2010), this would be complacent in the case of Formosa salmon given the known decline in range (Healey et al., 2001), and the logical extension to its abundance, levels of inbreeding, and genetic diversity. There has also been documented decline in genetic diversity (Hsu et al., 2015), and modelling indicates a similar future trajectory (Sato & Gwo, 2011).

Another recent concern regarding the genetic health of Formosa salmon has been the observation in 2016 of a mature male in the wild possessing phenotypic abnormalities, comprising a large head, small eye, unusual colouration, and a more pronounced hook on the maxilla (J. C. Gwo and S. Yamamoto, pers. comm., November 2017). Morphological deformation can result from inbreeding (Charlesworth & Willis, 2009), and has been observed in other small isolated salmonid populations (Sato, 2006; Tiira, Piironen, & Primmer, 2006). Although some might question whether this observation for Formosa salmon is any different from what might be expected for a genetically ‘healthy’ salmonid population, given the simultaneous low abundance and genetic diversity of Formosa salmon, and the empirical, theoretical, and simulation results from other systems (Pavlova et al., 2017), this is not the time to be complacent.

With clear established relationships between small and isolated populations, inbreeding, loss of genetic diversity, fitness, and population trajectories (Brook, Tonkyn, Q’Grady, & Frankham, 2002; Cnokrak & Roff, 1999; Frankham, 2005, 2010b; Spielman, Brook, & Frankham, 2004), there is a strong argument for the genetic rescue of Formosa salmon. Not all stream reaches separated by instream barriers have been genetically sampled, so it is possible that genetic novelty exists elsewhere in the system, but this seems unlikely given the limited spatial scale and recency of their isolation; however, this should be tested as a potential source of diversity for genetic rescue of individual stream reaches. If diversity is indeed lacking here, it can be introduced from non-Taiwanese populations of masu salmon (Gwo et al., 2008; Hsu, Wang, et al., 2010; S. Yamamoto, pers. comm., November 2017). This is fortuitous because in many imperilled taxa there are no close relatives, conspecific or otherwise, from which genetic diversity could be introduced, although using non-Taiwanese salmon may confer a risk of outbreeding depression.

Decision trees have been developed to indicate the risks of outbreeding depression during genetic rescue attempts. There is a greater risk if a population is taxonomically distinct, exhibits fixed chromosomal differences, occupies a substantially different environment, is genetically divergent, or has been genetically isolated for more than 500 years (Frankham et al., 2011; Weeks et al., 2011), and this framework has been recognized by the IUCN Species Survival Commission (IUCN/SSC, 2013). With respect to Formosa salmon, its level of taxonomic distinction and the potential presence of fixed chromosomal differences are at present unresolved. Although Formosa salmon can be distinguished genetically from other masu, divergence at putatively neutral loci poorly predicts outbreeding depression in fishes (McClelland & Naish, 2007). Although Formosa and other masu lineages are likely to have been isolated for more than 500 years, each of these considerations is merely a guide. Therefore, it is logical to test whether Formosa salmon can be crossed with other (landlocked) masu and produce viable offspring with elevated fitness, into future generations, rather than waste precious time debating taxonomies that may never be resolvable or investigating histories of isolation that in themselves are just proxies.

The main obstacle to overcome regarding the genetic rescue of Formosa salmon is the loss of ‘genetic identity’: by introducing genes from Japan or elsewhere, is it no longer ‘Formosa salmon’ (Love Stowell, Pinzone, & Martin, 2017)? This is a philosophical question, however, that should be addressed in the light of the decline already experienced by Formosa salmon, and its potential to persist despite low genetic diversity. As stated by Love Stowell et al. (2017), ‘For many endangered species, genetic purity is the problem and may be a prescription for extinction’. Furthermore, one should consider what it is that we seek to conserve.

1. The genetic identity of a population that reflects diversity lost, relative to others, rather than diversity gained (Weeks et al., 2016)?
2. A population that performs an ecological role in a specific location, in this case a top-order predator in high-elevation Taiwanese streams, regardless of its genetic identity (Meissner & Muotka, 2006)?

In essence, should we seek to conserve Taiwanese salmon or salmon in Taiwan?

Although the deferral of genetic rescue appears compatible with maintaining the genetic identity of a population, this can actually have the opposite effect. In some instances, the introduction of novel genetic diversity has been delayed until the last possible opportunity. For example, in 1986 the Norfolk Island Boobook Owl Ninox
of individuals released needs to be considered in the context of the biased sex ratio that already exists in the wild (Hsu et al., 2016), and also the potential implications for individual fitness (Havird et al., 2016). Subsequent generations from the wild should then be monitored to document changes in fish abundance and the frequency of introduced alleles in future generations (Hedrick & Fredrickson, 2010; Johnson et al., 2010). Guidelines for stocking rates already exist, such as a 20% contribution from the source population to the recipient population in the first instance (Weeks et al., 2011), and one individual per generation thereafter if an effective population size of 1000 cannot be maintained (Hedrick, 1995; Mills & Allendorf, 1996; Tallmon, Luikart, & Waples, 2004). The introduction of one migrant per generation will ensure future adaptation potential (Willi, Van Buskirk, & Hoffmann, 2006). These guidelines are also considered sufficient to protect any locally adaptive variation in the recipient population (Hedrick, 1995; Wang, 2004), supported by empirical observations (Fitzpatrick et al., 2015), but the specifics of reintroductions should still be considered on a case-by-case basis (IUCN/SSC, 2013). In this regard, simulations offer a means to determine optimal stocking and translocation rates (Pavlova et al., 2017; Pelletier et al., 2017). Stocking Chichiawan Stream with genetically pure Formosa salmon will not increase the genetic diversity of this population.

3.3 | Re-establish gene flow among populations to minimize future declines in genetic diversity

Gene flow should be re-established between populations that are bi- or uni-directionally isolated by artificial instream features (such as check dams), with uni-directionally isolated upstream populations being populations that can donate but not receive migrants, relative to downstream populations. The isolation of populations by check dams is a recent perturbation to Formosa salmon. These dams were erected for erosion control during the 1970s (Wang et al., 2013). Given the presence of at least six subpopulations isolated by check dams (Sato & Gwo, 2011), and in the absence of knowledge about downstream migration over these features, reciprocal exchanges should be conducted between all subpopulations. Although it has been recommended that exchanges should initially represent 20% of the recipient population (see above), this is not feasible with the number of pairwise exchanges required, but in this instance even exchanging several individuals between subpopulations will be useful (Hedrick, 1995; Weeks et al., 2011). The only caution is to ensure that there is no simultaneous spread of pathogens or other species (Hedrick & Fredrickson, 2010; IUCN/SSC, 2013).

The movement of Formosa salmon can be entirely facilitated and documented by managers, without the need to remove check dams. The direct movement of fishes by managers ensures the attainment of a specific rate of mixing, and an unambiguous interpretation of outcomes. Furthermore, the removal of check dams could unintentionally cause problems such as changes to flow regimes and invertebrate communities, or the spread of pathogens or other species that interact adversely with Formosa salmon. In 2011 the most downstream check dam in Chichiawan Stream was removed, which is a commendable
measure to increase the connectivity among salmon populations. The check dams in this stream are also filled with sediment and are therefore no longer capable of further erosion control. However, the removal of this check dam enabled an upstream expansion in the range of the shoveljaw carp (Onychostoma barbatulum), such that it now co-occurs with Formosa salmon (Chang et al., 2017). Although O. barbatulum is herbivorous and does not exhibit trophic overlap with Formosa salmon (Lin et al., 2012), there are suggestions that it may compete with Formosa salmon for habitat (Hsu et al., 2010) or disturb the Formosa salmon in other ways (e.g. by the disruption of nesting). The ecology of the possible interactions of these species should be examined.

It is important to note that assisted movement across check dams will only minimize the future loss of genetic diversity by increasing the effective population size (Hedrick & Fredrickson, 2010); it will not entirely prevent the continuing loss of genetic diversity, nor increase levels of diversity, if these populations are already genetically homogeneous. It is likely that increased genetic diversity can only be achieved by the introduction of alleles from outside the range of Formosa salmon.

3.4 Establishment of populations with independent risk susceptibilities

The contraction of Formosa salmon to a small range, and placement of the only captive population within the bounds of that range, presents high risk with respect to any stochastic and local perturbation within the Chichiawan Stream. As foretold by Healey et al. (2001), in 2004 the impact of a typhoon on the Chichiawan Stream triggered the unintended release of ~3000 hatchery fish into the wild that were descended from only 10 brood stock. This escape may be responsible for the subsequent decline in genetic diversity observed (Hsu et al., 2015).

In 2006 there were efforts to establish satellite populations in the wild (in Nanhu Creek, Sijie Lanxi, and Ikamaru Creek), first proposed at a meeting in 2000 (Healey et al., 2001). Satellite populations should be monitored and connected genetically to the original Chichiawan population via the direct movement of individuals. There are methods for identifying homologous habitat when choosing locations for satellite populations (Lentini, Stinemann, Stojanovic, Worthy, & Stein, 2018), and this could also extend to regions outside Taiwan. It is also worth noting, however, that improving the genetic health and fitness of individuals can expand the range of habitats within which they survive (Johnson et al., 2010).

4 Politics and pride

‘Politics and pride’ can become detrimental with respect to the conservation of isolated populations that are genetically, phenotypically, and geographically distinct. These can manifest at the level of parochialism for maintaining a species or population in its current state, despite the inability of the population to perform well in its present environment, and the fact that any genetic distinctiveness may only reflect its low abundance. These arguments were raised before the genetic rescue of Florida panthers, including the question of whether cross-bred individuals would still be afforded the same conservation status (in this instance, they were; Pimm, Dollar, & Bass, 2006). Similarly, motivations for minimizing human intervention and maintaining the intactness of the Isle Royale predator-prey study system, among other moral and ethical concerns, were raised with respect to the genetic rescue of the resident wolf population (Räikkönen, Vucetich, Peterson, & Nelson, 2009). Politics and pride can manifest in other ways, however. At the 2017 ‘International Symposium on the Discovery of Formosa Landlocked Salmon’s 100th Anniversary’ there were two emergent themes.

1. A lack of action by Taiwanese managers on the recommendations made at similar internationally attended meetings held in 2000 (Healey et al., 2001) and 2009 (Gold et al., 2010), several of which are repeated here.

2. A dearth of representation, presentation, information, and discussion involving Taiwanese managers and scientists that actually direct conservation efforts for Formosa salmon. This conference was logically held in Taipei, but given the lack of engagement by relevant managers it could equally have been held in Timbuktu.

Taiwan has a global responsibility to manage the population of salmonids in Chichiawan Stream, and the international scientific community – as exemplified by presentations at the 2017 meeting (Juanes, Rand, & Burridge, in press) – has the expertise, capability, and capacity to ensure that Taiwan can meet this goal.

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