

Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity ¹

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Abstract: Nearly 40% of commercial fisheries have now collapsed or are in serious decline. In response, governments have invested millions of dollars into artificial breeding programs, but many programs have failed to rehabilitate dwindling wild stocks. This failure may in part lie in the lack of knowledge about the genetic architecture of fitness: the genes and genotypes that are associated with individual performance. In this paper we discuss (i) artificial breeding programs, (ii) the genetic architecture of fitness, (iii) additive and nonadditive genetic effects on fitness, (iv) genetic diversity and evolvability, and (v) natural breeding and adaptation. We argue that most breeding programs do not maintain genetic adaptations and may consequently be ineffective at rehabilitating or enhancing wild populations. Moreover, there is no evidence that preserving genetic diversity as measured from neutral genetic markers increases fish performance or population viability outside of populations that experience strong inbreeding depression, and limited data that genetic diversity increases the potential for populations to adapt to changing environments. We suggest that artificial breeding programs should be used only as a last resort when populations face imminent extirpation and that such programs must shift the focus from solely preserving genetic diversity to preserving genetic adaptations.

Résumé : Presque 40 % des pêches commerciales se sont actuellement effondrées ou alors connaissent un important déclin. En réaction, les gouvernements ont investi des millions de dollars dans des programmes de reproduction artificielle; plusieurs de ces programmes n'ont pas réussi à rétablir les stocks en déperissement. Cet échec peut en partie s'expliquer par un manque de connaissance de l'architecture génétique de la fitness : les gènes et les génotypes associés à la performance individuelle. Nous discutons ici (i) des programmes de reproduction artificielle, (ii) de l'architecture génétique de la fitness, (iii) des effets génétiques additifs et non additifs sur la fitness, (iv) de la diversité génétique et de l'évolutibilité et (v) de la reproduction naturelle et de l'adaptation. Nous croyons que la plupart des programmes de reproduction ne préservent pas les adaptations génétiques et ainsi s'avèrent inefficaces pour rétablir ou renforcer les populations sauvages. De plus, il n'y a aucune indication que le maintien de la diversité génétique, mesurée par des marqueurs génétiques neutres, augmente la performance ou la viabilité de la population, à l'exception des populations qui connaissent une forte dépression consanguine; il y a des données restreintes qui indiquent que la diversité génétique augmente le potentiel des populations à s'adapter à des environnements changeants. Nous suggérons d'utiliser les programmes de reproduction artificielle seulement comme dernier recours lorsque les populations sont menacées d'extirpation imminente; ces programmes devraient être dédiés à la préservation des adaptations génétiques plutôt qu'à la seule conservation de la diversité génétique.

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Introduction

Capture fisheries are a major contributor to the global economy and food supplies. Worldwide, capture fisheries harvest more than 90 million tonnes of fish each year, with a value of approximately US\$90 billion (FAO 2009). These

fisheries provide direct employment to more than 30 million people, the majority of which are small-scale commercial or subsistence fishers that operate in inland or coastal waters (FAO 2009). Including the contributions of capture fisheries and aquaculture, fish accounts for 15% of the total animal protein consumed by humans and close to 20% of animal

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protein in low income, food deficit countries (FAO 2009). Fishes are a particularly important food source because they are rich in *n*-3 fatty acids, which are associated with health benefits that include reduced risk of coronary death and improved early neurodevelopment (reviewed by Mozaffarian and Rimm 2006). Given the enormous value of the capture fisheries, protecting commercially harvested stocks is a key priority for agencies around the world that are responsible for resource management.

Despite the importance of capture fisheries, global yields appear to have reached a plateau, with many individual stocks in decline. For the last 20 years, the yields of capture fisheries have fluctuated in the range of 85–95 million tonnes per year, and when data from China are excluded, yields have shown a modest decline during this period (FAO 2009). Furthermore, over the last 20 years, catches of more than a quarter of all fished species fell below 10% of their previous levels (Worm et al. 2006), which includes high profile collapses such as the crash of the Atlantic cod (*Gadus morhua*) (Myers et al. 1997). Although factors such as habitat degradation may contribute to declines in fishery yields, a number of studies have identified overexploitation as the primary threat to fisheries sustainability (e.g., Jackson et al. 2001; Pauly et al. 2002; Myers and Worm 2003). Indeed, the Food and Agriculture Organization of the United Nations (FAO) has estimated that 28% of marine fisheries produce less than their maximum potential, owing to current or past overexploitation (FAO 2009; also see Hutchings et al. 2010). In contrast, only 2% of stocks are underexploited, with the remaining 70% of stocks either moderately or fully exploited (FAO 2009). Preserving existing fisheries and restoring depleted stocks are thus key objectives for conserving the global fisheries at what is likely the maximum yield of about 90 million tonnes annually.

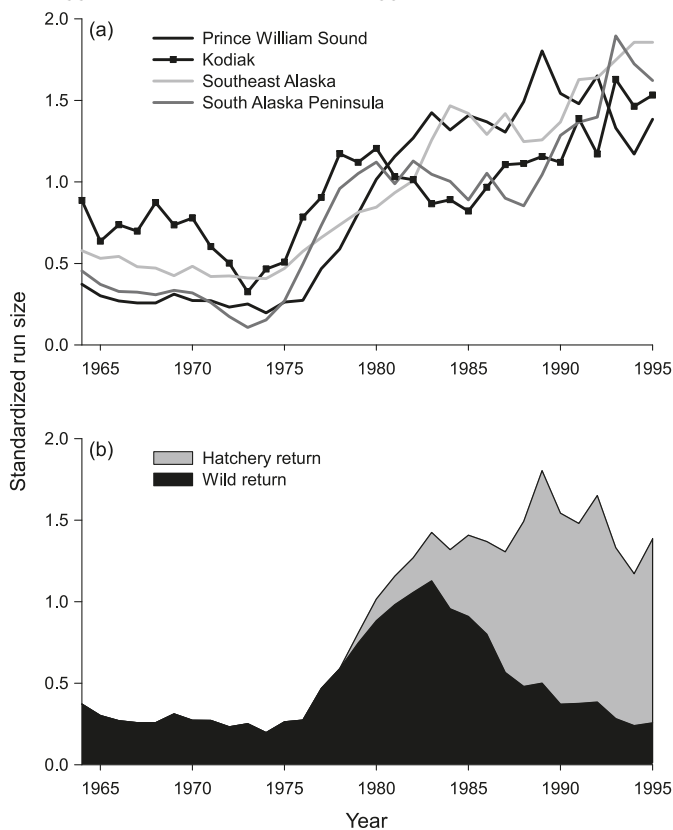
Artificial breeding programs are common tools that are used in fishery management to augment or rehabilitate dwindling wild stocks (see Appendix A for definition of this and other terms used in this paper). These programs have the potential to increase stock sizes when populations are limited by juvenile recruitment and have been applied to a variety of fishery issues that include (Utter and Epifanio 2002): (i) to supplement declining populations and maintain genetic diversity so as to reduce the risk of local extinction; (ii) to preserve existing fisheries when anthropogenic activity, such as the construction of dams, degrades spawning habitat and disrupts natural ecological processes; and (iii) to enhance already healthy stocks of wild fish to provide additional opportunities for recreational or commercial fishers. Artificial breeding programs have been used to manage a wide range of fisheries such as Atlantic cod, flounder (*Paralichthys olivaceus*), and red sea bream (*Pagrus major*) (Masuda and Tsukamoto 1998; Svåsand et al. 2000). However, it is with salmonids that artificial breeding programs have been used most extensively as part of management strategies. Each year salmonid hatchery programs release more than 4.5 billion juvenile salmon into natural waters at a significant economic cost ranging up to about 100 million dollars (Hilborn 1998; Naish et al. 2008).

Despite the extensive use of artificial breeding programs for augmenting salmonid stocks, the effectiveness of the programs in meeting management goals is still poorly under-

stood. Breeding program effectiveness remains poorly understood in part because the ubiquity of hatcheries on salmon bearing rivers makes it difficult to identify comparison populations without hatcheries and thus to conduct appropriately controlled scientific studies. For example, a recent evaluation of Pacific salmon (*Oncorhynchus* spp.) hatchery programs in the continental USA found that similar nonsupplemented populations could be identified for only 8 of the 22 hatcheries examined (Waples et al. 2007). Of those eight hatcheries, five (63%) supplemented populations had trends in abundance that were comparable to control populations, one (12%) supplemented population had lower abundance than its paired control population, and only two (25%) supplemented populations outperformed the paired control populations (Waples et al. 2007). A study of hatchery enhancement of pink salmon (*Oncorhynchus gorbuscha*) in Alaska similarly failed to provide clear evidence that artificial breeding programs were effective (Hilborn and Eggers 2000). Hatchery supplementation in the Prince William Sound and Kodiak Island areas of Alaska began in the mid-1970s, and by 1990, the annual releases in these areas exceeded a combined 600 million fry. Over this same period, salmon returns increased by a factor of about two, and generally the programs were touted as a success. However, Hilborn and Eggers (2000) also assessed the performance of pink salmon in two control sites comprising southeast Alaska and the South Alaska Peninsula, two other pink salmon producing regions in Alaska that neighbour Prince William Sound and Kodiak Island but that have never been subject to significant augmentation from artificial breeding programs. Comparing pink salmon abundance in the two control regions revealed that natural stocks increased at a similar rate to the artificially “enhanced” regions (Fig. 1a). Thus, the trends in abundance did not support a clear benefit of the artificial breeding programs. Moreover, when the contributions of wild and hatchery bred fish to the total run were compared in Prince William Sound and the Kodiak Island area, it became apparent that hatchery fish had largely replaced their wild counterparts in the most supplemented region, leading to a sharp decline in wild fish despite stable overall population size (Fig. 1b; Hilborn and Eggers 2000). These data suggest that artificial breeding programs for pink salmon in Alaska have largely led to replacement of wild fish with hatchery-bred fish as opposed to a clear enhancement of population size.

One area in which artificial breeding programs appear to have been successful is in the preservation of critically endangered populations. For example, aurora trout (*Salvelinus fontinalis timagamiensis*) were extirpated from the wild during the 1960s as a consequence of lake acidification in northern Ontario (Snucins et al. 1995). However, these fish escaped extinction, thanks to a hatchery program founded with nine individuals in 1958, which allowed the trout to persist in captivity and eventually be reintroduced to their native habitat (Snucins et al. 1995). The artificial breeding program for Chinook salmon (*Oncorhynchus tshawytscha*) in the Sooes River similarly appears to have been successful, as it was associated with a 10-fold increase in population size, from a low of less than 100 fish returning annually (Brannon et al. 1999; for additional examples see Brannon et al. 2004). Artificial breeding programs may thus be an important tool when populations are at risk of imminent extinction, but de-

Fig. 1. Run sizes of Alaskan pink salmon (*Oncorhynchus gorbuscha*) in relation to hatchery supplementation. (a) Run size of pink salmon in areas that received hatchery supplementation starting in 1975–1976 (Prince William Sound and Kodiak Island) and in areas that did not receive hatchery supplementation (southeast Alaska and the South Alaska Peninsula). (b) Contribution of hatchery and wild fish to the total returns of pink salmon in Prince William Sound. In both graphs, run sizes are presented as 5-year running averages that are scaled by the 1976–1985 average values in each area. The figure was redrawn from data presented in Hilborn and Eggers (2000) and Hilborn and Eggers (2001).



spite some notable successes, these programs have generally had low success at restoring stable populations in the absence of continued supplementation (Griffith et al. 1989; Fischer and Lindenmayer 2000).

Artificial breeding programs may also have unintended consequences that threaten the persistence of naturally occurring stocks. In salmonids, artificial breeding programs have been associated with negative effects on a number of important characteristics in the hatchery propagated fish. For example, hatchery-raised salmon show reduced foraging efficiency on live prey, reduced sensitivity to predation risk, and increased aggressiveness relative to wild individuals (e.g., Sundström and Johnsson 2001; Álvarez and Nieceza 2003; Sundström et al. 2003). These behavioural shortcomings may have considerable consequences for the fitness of hatchery fish. For example, the reproductive success of hatchery bred steelhead trout (*Oncorhynchus mykiss*) has been estimated to decline by about 40% for each generation of artificial breeding (Araki et al. 2007). Moreover, reproductive success was lower in wild born steelhead trout that had at

least one hatchery-bred parent, which indicates a genetic basis to the reduced performance of hatchery fish (Araki et al. 2009). Artificially propagated fish may thus have serious negative effects on the genetic quality of wild fish when the two groups interbreed, which can threaten the genetic integrity and sustainability of wild populations (Ford 2002; Fraser 2008).

In this paper we review the approaches and objectives of artificial breeding programs with a focus on genetic aspects of fitness. We argue that current breeding programs are too focused on genetic diversity and thereby fail to acknowledge the complexities of the genetic architecture of fitness of wild populations. We detail these complexities and make broad, multi-tier recommendations to revamp the approach to management of wild fish populations, as well as make specific recommendations on how to conduct artificial breeding programs to maintain the genetic integrity and sustainability of wild populations. We begin by detailing the fertilization methodology used in current artificial breeding programs. We follow that section with an overview of the genetic architecture of fitness and the contributions of additive and non-additive genetic effects to fitness and population viability. Finally, we discuss the role of natural mating in promoting and maintaining healthy gene pools.

Artificial breeding programs and fertilization methodology

Artificial breeding programs for fishes use either captive breeding or supportive breeding approaches. The breeding approach used depends on several factors, most notably the size and conservation status of the remaining wild population (Miller and Kapuscinski 2003; Kapuscinski and Miller 2007). When remaining populations are small and facing imminent extirpation or extinction, a captive breeding scheme is typically employed. Captive breeding brings into captivity a large proportion of the remaining individuals for the purpose of rearing subsequent generations for eventual re-release into the wild. In contrast, when remaining populations are more stable, but are either likely to become threatened in the near future or enhancement for increased harvest is desired, a supportive breeding scheme is a more common strategy. Supportive breeding is the practice of bringing into captivity only a small fraction of individuals from the wild for reproduction, for all or part of their life cycle, and then returning their offspring into their native habitat where they join their wild-produced counterparts (Ryman and Laikre 1991).

There are many genetic risks associated with the use of artificial breeding programs (reviewed in Miller and Kapuscinski 2003; Campton 2004; Fraser 2008). One risk that has attracted the most attention is the loss of genetic diversity (e.g., Hedrick 2001; Fiumera et al. 2004). Theoretical work indicates that this loss of genetic diversity stems from a reduction in effective population size mediated by an increase in variance in reproductive contribution among individuals (Ryman and Laikre 1991; Wang and Ryman 2001). Consequently, the most common breeding programs used today focus on the retention of genetic diversity through the maintenance of effective population size. These programs can be classified into four basic fertilization approaches: (i) mass mating; (ii) single-pair mating; (iii) nested mating; and (iv) factorial mating.

First, mass mating designs involve taking gametes from multiple members of each sex or multiple members of one sex and a single individual of the other sex, and mixing them together to achieve fertilization. For example, it was once common practice to employ a form of a mass mating design known as the “mixed-milt approach”, where milt from several males was used simultaneously to fertilize the eggs of a single female. This protocol was initially popular because it was appropriate for broodstocks of all sizes, it was easy to accomplish, and hatchery managers believed it helped to ensure fertilization of the eggs in the event that one of the males’ milt was either compromised during collection or functionally infertile. However, this practice has been eliminated from many programs because of the realization that this mating scheme can result in smaller effective population size owing to the differences in fertilization rates of the males, which arises from differences in the ability of males to succeed at sperm competition. For example, several studies on salmonid species, including Chinook salmon (Withler 1988; Withler and Beacham 1994), Atlantic salmon (*Salmo salar*) (Gage et al. 2004; Yeates et al. 2007), pink salmon (Gharrett and Shirley 1985), and coho salmon (*Oncorhynchus kisutch*) (T.E. Pitcher, D.D. Heath, and S. Al-Smoudi, unpublished data), have shown skewed paternity among competing males in mixed-milt fertilization trials. The differences in competitiveness has been directly attributed to variation in sperm density, velocity, and longevity among males (e.g., Hoysak and Liley 2001; Gage et al. 2004; Pitcher et al. 2009).

It is possible that sperm competition could increase offspring genetic quality if males that achieve higher fertilization success are also more effective in producing viable offspring (i.e., that there is heritable variation among males in their general viability or condition and that this variation is associated with that male's success in sperm competition — the so called “good-sperm hypothesis”; Yasui 1997). However, empirical support for the good-sperm hypothesis is limited (e.g., Hosken et al. 2003; Fisher et al. 2006; Simmons and Kotiaho 2007), and this hypothesis has yet to be tested in fishes. Thus, it is unclear whether sperm competition can improve genetic quality, yet it clearly results in unequal genetic contributions from males and lower effective population sizes than if the contributions were normalized. Indeed, Wedekind et al. (2007) attempted to experimentally assess the effect of sperm competition on effective population size in Alpine whitefish (*Coregonus zugensis*) and estimated that it could decrease the effective number of male breeders by up to 50%. Because of concerns about the negative effect that mass mating, and specifically sperm competition, has on effective population size, these kinds of spawning protocols have been removed from spawning guidelines for many hatcheries (e.g., Pacific salmon hatcheries in the Columbia River basin: Integrated Hatchery Operations Team 1995).

Second, single-pair mating designs, also known as a pairwise mating design, where one female and one male are used to produce offspring, is a popular technique in many hatcheries today because it gives each parent an equal opportunity to contribute genetically to the offspring gene pool owing to a lack of sperm competition. One of the major problems with this mating design is that if either parent is functionally infertile owing to, for example, poor sperm or

egg quality, neither of the parents will contribute genetically to the pool of offspring. As such, this kind of mating design is typically recommended for larger broodstock programs in which the number of male and female adults available for spawning is sufficient to ensure a large effective population size despite the loss of a few of the crosses because of poor gamete quality (Campton 2004).

A variation of the single-pair mating design involves overlapping pairwise spawning schemes, where milt from a primary male is mixed with the eggs from one female, and the mixture is allowed to sit for a period of time before the milt from a second male is added in case the primary male has poor sperm quality. In a second spawning, the secondary male from the first mating becomes the primary male and the other male becomes the secondary male. This mating design assumes that the interval between the addition of sperm from the first and second male is sufficient to ensure that the first male has sperm precedence and will fertilize most of the eggs unless he is functionally infertile whereby the second male will garner all of the paternity. Recent work on Atlantic salmon has shown that just a two second delay between the release of the first and second males’ milt can be sufficient to ensure that the first has sperm precedence and fertilizes most of the eggs (Yeates et al. 2007). However, breeding programs employing this overlapping scheme typically employ a delay of between 10 and 30 s (Withler and Beacham 1994).

Third, nested mating designs typically involve crossing a member of one sex with two or more members of the other sex. For example, one male may be crossed independently with each of three females or one female may be crossed with each of three males. This design is most commonly used when a single-pair mating scheme is not possible because of a strong skew in the sex ratio of parents. To compensate for skewed sex ratios, individuals from the less abundant sex are mated with two or more individuals of the more abundant sex. Importantly, unlike the mass mating scheme, nested mating schemes do not pool the milt but instead perform separate fertilization events with each additional mate. Consequently, sperm competition is eliminated and reproductive contributions from the broodstock are normalized within each sex. A drawback to the skewed sex ratio is that effective population size decreases dramatically with increases in the skew.

Fourth, more recently a full factorial mating design, which is also known as the matrix mating design, has been used (reviewed in Neff and Pitcher 2005; Busack and Knudsen 2007). In this design, males and females are crossed in all possible combinations. For example, Pitcher and Neff (2007) examined a variety of scenarios regarding supportive breeding for Chinook salmon using an 11 × 11 full factorial mating design. They split the eggs from each of 11 females into 11 batches of equal numbers and, for each female, fertilized each batch with milt from a different male. Thus, for a given female, 11 paternal half-sib families were generated. Assuming there are limited amounts of infertility, the underlying premise of the full factorial mating design is that each adult selected should have an equal opportunity and probability of producing an equal number of progeny with each potential mate, which in theory maximizes the number of genetic lineages produced. The full factorial mating design also has the advantage of facilitating the assessment of genetic and envi-

ronmental components of phenotype and performance based on measurements taken of the offspring from the various families (e.g., Pitcher and Neff 2007; Wedekind et al. 2008). Despite these potential benefits, full factorial mating designs are not commonly used because they are logistically more difficult and expensive to conduct than the other three methods. To alleviate these problems, Withler and Beacham (1994) proposed a modified factorial mating design where eggs from n females are combined, mixed thoroughly, then split into n batches with each batch being fertilized by a different male. This modification reduces the number of fertilization events by a factor of n . However, it has the downside of potentially transmitting disease amongst eggs from different females and it negates the potential to examine genetic and environmental components of offspring phenotype, at least without reconstructing pedigrees using genetic markers. In addition, factorial mating designs in general have met some resistance by hatcheries because of a concern that the design can increase inbreeding depression because of the large numbers of half-sib families that are generated. However, such concerns are not supported by theoretical models, which show that inbreeding levels are instead reduced over multiple generations with either full or partial factorial mating designs (Engström et al. 1996; Dupont-Nivet et al. 2006).

Several attempts have been made to empirically and theoretically assess the efficacy of conducting single-paired matings versus partial or full factorial matings to maximize the effective number of breeders and ultimately the effective population size. Fiumera et al. (2004) used a factorial breeding design based on a modelling approach to implement an artificial breeding program for redhorse (*Moxostoma robustum*), an endangered North American cyprinid. They found that factorial mating can increase effective population size by nearly 20% and much of the benefit is achieved with as little as a series of 2×2 matings. In a second study, Dupont-Nivet et al. (2006) used a simulation approach to examine the utility of different mating designs to preserve genetic variability in populations undergoing selection. They found that a selection response was improved and inbreeding depression was reduced over multiple generations of a full factorial mating design and, again, that even just 2×2 crosses were superior to single-pair matings. Finally, Busack and Knudsen (2007) used simulations to examine the utility of four full factorial mating designs, 10×10 , 20×20 , 40×40 , and 120×120 , and three partial factorial mating designs, 2×2 , 5×5 , and 10×10 , to maximize the effective number of breeders. They found that partial factorial mating in all but the smallest crosses achieved no less than half of the number of breeders and often a nearly equivalent number of breeders as the analogous full factorial design, and concluded that in practice there is often little need to consider full factorial designs. Partial factorial crosses thus provide artificial breeding programs with a logistically feasible breeding scheme that can maintain effective population size and maximize the number of genetic lineages.

Genetic architecture of fitness

A major caveat in many artificial breeding programs is the sole focus on effective population size and the maintenance of genetic diversity. This approach ignores many of the complexities that underlie the genetic architecture of fitness and

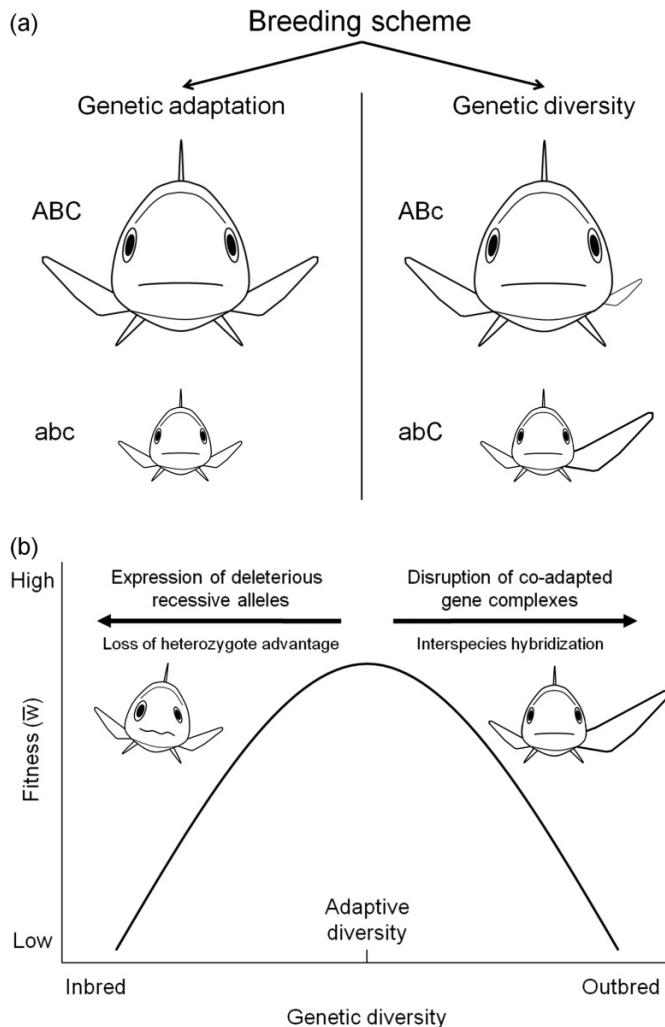
local adaptation. We argue that to maintain healthy wild populations, breeding programs must target the genes underlying fitness as opposed to genetic diversity per se, and to do so, we must have an understanding of the genetic architecture of fitness within populations.

The genetic architecture of fitness has two components that can be referred to as good genes and compatible genes (Neff and Pitcher 2005). A good gene is defined as a gene variant or allele that increases fitness independent of the architecture of the remaining genome, which, in diploid organisms, includes the homologue to the particular “good allele”. Across the genome, good genes will show additive genetic variance. Thus, when variation exists among individuals in good genes quality, the population can respond to directional selection on fitness (for a review of additive genetic effects in salmonids see Carlson et al. 2008). A compatible gene is defined as an allele that increases fitness when in a specific genotype (i.e., when paired with a specific homologue (overdominance) or an allele at another gene locus (epistasis)). Across the genome, compatible genes show nonadditive genetic variance and the population does not respond to directional selection on this component of fitness. In the case of epistasis, compatible genes can take the form of a co-adapted gene complex, in which case an individual allele has either a positive or negative effect on fitness depending on the composition of the rest of the genome (Fig. 2a). In fishes, co-adapted gene complexes likely underlie complex traits such as foraging polymorphisms, which consist of a suite of morphological and behavioural characteristics that are adaptive only in specific combinations. For example, in threespined sticklebacks (*Gasterosteus aculeatus*), two morphologically distinct ecotypes are present in many lakes, with one adapted to feeding in open water habitat and the other to feeding in benthic habitat (Schluter 1993). Hybrid offspring of the two morphs are morphologically intermediate and have low foraging success and slow growth in either habitat (Schluter 1993, 1995). In conjunction with inbreeding depression, compatible gene effects can define an optimal level of diversity within individuals and populations (Fig. 2b; for examples, see Marshall and Spalton 2000; Neff 2004a).

The fitness contribution of an allele or genotype can be assessed by its contribution to an individual's lifetime reproductive success (LRS). Lifetime reproductive success is composed of both survivorship and breeding success: $LRS = \sum l_x \times m_x$, where l_x is the survivorship to age x , m_x is the breeding success as measured by the number of offspring that an individual produces at age x , and the summation is over an individual's lifetime (Stearns 1992). Individuals that have alleles or genotypes that are associated with either high survivorship or high breeding success will have higher fitness than individuals that have alleles or genotypes associated with low survivorship and breeding success. Because the effect that an allele or genotype has on fitness can vary across environments — referred to as a gene by environment interaction — fitness must be assessed in the context of the individuals' natural environment.

Studies of the genes of the major histocompatibility complex (MHC) have provided some of the best examples of both good and compatible gene effects (reviewed by Potts and Wakeland 1990; Apanius et al. 1997; Bernatchez and Landry 2003). The MHC is found in all jawed vertebrates

Fig. 2. Relationships among epistasis, genetic diversity, and fitness. (a) A hypothetical example of compatible gene effects arising from epistasis on fitness. For simplicity, genetic diversity is modeled for three haploid loci (A,B,C), which determined body size, right pectoral fin size, and left pectoral fin size, respectively. Each locus displays additive effects on morphology with the uppercase allele associated with large size and the lowercase allele associated with small size. In the breeding scheme on the left, genes are preserved in combinations that complement each other and maintain co-adapted gene complexes (high fitness). In contrast, the breeding scheme on the right preserves the same amount of genetic diversity, but because the genetic architecture of fitness is not considered, co-adapted gene complexes are disrupted and maladaptive phenotypes are produced (low fitness). Understanding the genetic architecture of fitness is thus critical in the design of breeding programs. (b) Expected relationship between genetic diversity and fitness. At low levels of genetic diversity, fitness is reduced by inbreeding depression, which arises from the expression of deleterious recessive alleles and the loss of heterozygote advantage. At high levels of genetic diversity, fitness is reduced by outbreeding depression, which arises from the disruption of co-adapted gene complexes and low viability of interspecies hybrids.



and often includes a cluster of genes broadly classified into either the class I or class II types (in humans, the MHC is referred to as the HLA or human leukocyte antigen). The

protein products of these genes are involved in immune response regulation. In many populations, the MHC is highly polymorphic and most individuals are heterozygous at the coding loci, presumably because those heterozygous individuals are able to present a wider range of foreign peptides to T-cells and thereby have a selective survivorship advantage over homozygous individuals (Klein and Figueroa 1986). In such cases, nonidentical homologues at either the class I or II genes can be considered compatible genes.

As an example, Arkush and colleagues (2002) used in vitro fertilization techniques with Chinook salmon to produce individuals that differed in their diversity at the MHC. Specifically, they were able to generate full-siblings that were either homozygous or heterozygous at the MHC class II set of genes. The researchers then exposed the families to infectious hematopoietic necrosis virus (IHNV). IHNV causes epizootics in salmonids and is considered to be one of the most important viral pathogens affecting these fish in North America (see Arkush et al. 2002). They found that for 7 of 10 families, survival was higher in the heterozygous siblings than the homozygous siblings, and they calculated the selection advantage of heterozygous individuals to be just under 10%. Their experimental approach was particularly powerful because by comparing full siblings carrying different MHC genotypes, the effects due to other segregating genes were minimized.

The MHC also provides an excellent example of good genes and serves to illustrate the distinction between good genes and compatible genes. Lohm et al. (2002) investigated interactions between specific MHC alleles and resistance to bacterial infection by *Aeromonas salmonicida* in Atlantic salmon (*Salmo salar*). Full-sibling broods were generated that contained individuals with different combinations of alleles. The researchers focused on two alleles, referred to as *e* and *j*. In the first experiment they generated siblings that were *e*+/+, *j*+/+ and *e**j*, where the + represents an allele other than *e* or *j*. Over an 18-day period post infection, they found that *j*+/+ individuals had the lowest survivorship, while *e*+/+ and *e**j* individuals had similar levels of survivorship. In a similar second experiment they generated siblings that were *e**e*, *j**j* and *e**j* and found that *j**j* individuals had the lowest survivorship, while *e**e* and *e**j* individuals had similar levels of survivorship. In this study, MHC heterozygosity was not important for increasing fitness, but possessing the *e* allele was important for increasing fitness. Indeed, Lohm and colleagues (2002) calculated the fitness advantage of possessing the *e* allele to be as high as 49%. Thus, in a population challenged predominately by *A. salmonicida*, the *e* allele would confer a fitness advantage and thereby represents a good gene. A similar result has been demonstrated in Alpine whitefish (Wedekind et al. 2004).

Additive and nonadditive genetic effects on fitness

Given that the genetic architecture of fitness has two components, it is important to understand the relative contributions of these components to variation in fitness in natural populations. Full factorial mating designs are one of the best ways to simultaneously measure the contributions of additive and nonadditive genetic variation to a trait (Lynch and Walsh 1998). Because full factorial designs mate a group of parents in all possible pairwise combinations and then compare the

Table 1. Summary of two-way analysis of variance (ANOVA) results from a full factorial breeding experiment in Chinook salmon.

Source	df	<i>F</i>	Variance ($\times 10^{-2}$)	Ttotal variance (%)	Genetic variance (%)
Dam	10, 100	41.0	2.55	12.4	Maternal environmental 9.7
Sire	10, 100	9.0	0.56	2.7	Additive 10.8
Dam×Sire	100, 24 200	11.2	0.62	3.1	Nonadditive 12.4
Total	24 200		20.6		

Note: Additive genetic variance was calculated as four times the percent of total variance captured by the sire component, nonadditive genetic variance was calculated as four times the percent of total variance captured by the dam \times sire component, and maternal environmental variance was calculated from the difference between the dam and sire component (Lynch and Walsh 1998). Genetic variance values are expressed as a percent of the total variance in survivorship. *P* values for all components were significant at $P < 0.001$. The results include source of variation in survivorship, degrees of freedom (df), *F* statistic, variance component, percentage of total variance, and genetic variance estimates. The data are from Pitcher and Neff (2007) and were reanalyzed following the methods in Puurtinen et al. (2009).

progeny from each family, variance associated with a trait can be partitioned into effects of the dam (maternal environmental effects and maternal additive genetic effects), the sire (paternal additive genetic effects), and the interaction between the dam and sire (nonadditive genetic effects). A recent review of 24 studies that used full factorial mating designs in a range of taxa found that the relative contribution of additive and nonadditive genetic effects on fitness-related traits were approximately equal, although the authors of the review were unable to calculate the absolute magnitudes from those studies (Puurtinen et al. 2009). Using the methods described by Puurtinen et al. (2009) and the data on Chinook salmon from Pitcher and Neff (2007) as one example, we found that additive and nonadditive genetic effects captured 10% and 12%, respectively, of the variance in early-life survivorship (Table 1). These studies collectively suggest that both additive and nonadditive genetic effects are important contributors to the genetic architecture of fitness.

Nonadditive genetic effects on fitness may arise from inbreeding depression, overdominance, or epistasis. Inbreeding depression occurs when the progeny of related parents have lower fitness than the progeny of unrelated parents. Inbreeding depression has been documented in a wide range of natural populations and generally arises as a consequence of small effective population sizes (Hedrick and Kalinowski 2000; Keller and Waller 2002). Inbreeding is thus a concern for many breeding programs because of its prevalence in threatened populations. Indeed, an examination of 170 threatened species found that genetic diversity was lower in the threatened species than in taxonomically related species that were not threatened for 77% (131) of comparisons. Specifically, heterozygosity at allozyme and microsatellite loci was about 35% lower in the threatened species than the nonthreatened species, albeit the fitness consequences of this reduced diversity were not measured (Spielman et al. 2004). In salmonids, inbreeding depression has been demonstrated for a number of fitness-related traits, but most studies have been done in captive environments using acute inbreeding between close relatives (Wang et al. 2002). Examining the consequences of inbreeding in wild populations that experience a gradual increase in the relatedness of breeding pairs over time, as might be the case for populations in decline, will be critical to determine the importance of inbreeding depression as a nonadditive genetic component of fitness in wild populations. Indeed, salmonids in particular may be somewhat buffered from the effects of inbreeding as compared with some other

fishes because they have two copies of many genes (i.e., up to four alleles per individual) as a result of an ancestral genome duplication (Allendorf and Thorgaard 1984).

Nonadditive genetic effects can also influence fitness through overdominance. While there are several examples of strong overdominance effects at individual loci, such as the MHC described above, studies examining genome-wide levels of overdominance suggest that it has only a small effect on fitness. Such genome-wide effects have most commonly been assessed in large, outbred populations using heterozygosity–fitness correlations (reviewed by Coltman and Slate 2003; Hansson and Westerberg 2008; Chapman et al. 2009). A recent meta-analysis of over 600 reported correlation effect sizes from 73 studies showed only a small effect, with multilocus heterozygosity explaining less than 1% of the variance in life-history, morphological, and physiological traits (Chapman et al. 2009). These data might suggest that overdominance is a relatively insignificant component of fitness. However, the weak relationship probably arises in part because of the small number of microsatellite loci typically used to estimate heterozygosity–fitness correlations. Diversity at a small number of marker loci provides a reliable estimate of genome-wide heterozygosity only when there is strong identity disequilibrium between the marker loci and the rest of the genome, such as may be caused by inbreeding or admixture of different populations (Ljungqvist et al. 2010). Additionally, small numbers of marker loci are unlikely to capture strong overdominance effects at individual fitness-related loci, because recombination disassociates alleles at the marker loci from those of the fitness locus (Balloux et al. 2004). The studies examined by Chapman et al. (2009) may also fall on either side of an optimal level of genetic diversity (Fig. 2b) and thus capture both inbreeding depression and outbreeding depression, the effects of which may partially cancel out in the meta-analysis. Thus, although it is now recognized that a small number of neutral loci are unlikely to effectively estimate genome-wide levels of heterozygosity, the actual contribution of heterozygosity and overdominance to fitness, particularly at individual loci, is not yet well understood.

Nonadditive genetic effects may also arise from epistasis, which occurs when the effects of an allele are modified by an individual's genetic composition at other parts of the genome. For example, adaptive pigmentation differences in beach mice (*Peromyscus polionotus*) are determined by the genes of both the *melanocortin-1 receptor* (*Mclr*) and *Agouti*

signaling protein (*Agouti*), but *Mclr* has an observable phenotypic effect only when individuals also possess a specific *Agouti* allele (Steiner et al. 2007). Epistasis may also arise from co-adapted gene complexes such as foraging polymorphisms as we have described above (Schluter 1993, 1995). In practice, it is statistically challenging to detect epistasis because the number of potential epistatic interactions between a group of genes is exponentially greater than the number of potential additive effects of those genes. Consequently, the importance of epistasis is not well understood outside of a few model systems (e.g., Tong et al. 2004).

Additive genetic variance, on the other hand, has been well studied, particularly within the salmonids. In those fishes, additive genetic variance has been documented as a component underlying a wide range of morphological, physiological, and life-history traits (for reviews see Garcia de Leaniz et al. 2007; Carlson and Seamons 2008). Additive genetic variance is often estimated from calculations of narrow sense heritability. For example, a review of 185 studies of salmonids found that estimates of the narrow sense heritability was highest for morphological traits ($h^2 = 0.29$), moderate for behavioral ($h^2 = 0.20$) and physiological traits ($h^2 = 0.19$), and lowest for life-history traits ($h^2 = 0.16$) (Carlson and Seamons 2008). Some caution is warranted when using heritability values to estimate additive genetic variance, because considerable additive genetic variation can exist even for traits with low heritability when there is large phenotypic variation. Consequently, low heritability of a trait does not necessarily translate into low additive genetic variance for that trait. Nevertheless, the studies on salmonids indicate that additive genetic variation can be an important component of fitness.

Genetic diversity and evolvability

What about the importance of maintaining genetic diversity for evolvability and future adaptation to a changing environment as opposed to for fitness in a current environment? Several researchers have postulated that populations with greater standing genetic diversity will be more likely to persist in changing environments, particularly those that result from anthropogenic activities such as climate change, than populations with lower standing genetic diversity (Lande and Shannon 1996; also see Petrie and Roberts 2007; for a review, see Colegrave and Collins 2008). For example, the oceans of the east and west coasts of Canada are predicted to increase in temperature over the next 50 years (IPCC 2007) and captive populations that maintain large amounts of genetic variation may have individuals with genotypes that are better suited for the anticipated warmer waters. While the idea may seem straight forward — it is more probable that a population with increased diversity will have an individual with a gene or gene variant that is better suited for some aspect of an altered environment than a population with decreased diversity — there is surprising little empirical evidence and none from fishes to support the claim.

Although we do not dispute that reduced genetic diversity can result in increased inbreeding depression, which in itself can reduce population viability and persistence (e.g., Markert et al. 2010), we emphasize here that there is limited data linking genetic diversity and the ability of a population to adapt and persist in a new environment (i.e., independent of the effects of inbreeding depression; for additional discussion

of this point see Willi et al. 2006). To our knowledge, there is only a single experimental study to examine the role of genetic diversity and population adaptability to a novel environment in a sexually reproducing animal. Using laboratory populations of *Drosophila melanogaster*, Reed et al. (2003) tested the importance of genetic diversity and lineage on adaptability to a novel, stressful environment. They found that outbred populations showed a greater response in fitness, as measured by the number of progeny, than inbred populations when exposed to a sugarless growth medium for seven generations. Importantly, the effect was observed on the absolute increase in the number of progeny from the first to seventh generation, and thus their measure controls for differences in the starting number of progeny produced by the two types of populations. That is, although the outbred populations produced more offspring from the initiation of the experiment, those populations also showed a greater response and presumed adaptation to the sugarless diet through the seven generations of selection. Interestingly, the authors also found that populations that had been previously exposed to a different stressful environment (the presence of a toxin in the medium) were more likely to show positive fitness gains when exposed to the novel stressor. The authors also found strong lineage effects and lineage by environment interaction effects, which indicate a degree of unpredictability in the evolvability of populations based on the specific lineages that are used to found the population.

Other evidence for the importance of genetic diversity for population evolvability comes from correlational data. For example, Saccheri et al. (1998) studied a large metapopulation of butterflies (*Melitaea cinxia*) and found that the extinction risk increased significantly with decreasing heterozygosity, as measured using seven allozyme loci and one microsatellite locus, owing to reduced egg hatching rates, larval survival, and adult longevity. The data suggest that populations with increased genetic diversity are better able to persist, presumably because of continued adaptation to their environment. However, a later study showed that population growth was actually related to variation in just one of the allozyme loci. That gene locus coded for an enzyme involved in glucose metabolism and the resupply of energy to muscles during flight (Hanski and Saccheri 2006). Interestingly, the other six allozyme loci showed no evidence of overdominance, so it is unclear what drove the original pattern between population viability and multilocus heterozygosity. Regardless, there is remarkably scant data on the relationship between genetic diversity, population viability, and evolvability. Furthermore, studies of microbes indicate that evolvability stems from new mutations and not standing genetic variation (e.g., Lenski et al. 1991; Elena and Lenski 2003) and thereby suggest that maintaining genetic diversity is less important than increasing the rate of mutations. Of course microbes have vastly different biology from fish, and thus it is difficult to draw too much inference from the microbe studies. Yet other data shows both persistence and adaptation in populations that have experienced long-term bottlenecks and loss of genetic diversity (e.g., Lehman 1998). Clearly, more empirical studies are needed to understand the role of genetic variation in evolvability and its consequences for artificial breeding programs.

Natural mating and genetic adaptation

One of the major goals for most artificial breeding programs is to maintain genetic diversity by maximizing the effective population size, but reaching this goal often comes at the cost of reduced genetic fitness (Fraser 2008). Indeed, this objective has been criticized because it is not based on biological mechanisms found in natural mating systems (Tregenza and Wedell 2000; Pitcher and Neff 2007). Quinn (2005) points out that the fundamental problem with salmonid artificial breeding programs is that natural selection and sexual selection are essential for the continued viability of a population in the wild, yet no breeding design in a hatchery can possibly mimic these natural processes. For example, in salmonids, gravid females choose and prepare nest sites, males compete intensely for access to females, females spawn with a single or multiple males, which can promote sperm competition, and then those eggs are buried in the substrate until the fry emerge months later. It is interesting that natural and sexual selection almost invariably leads to nonrandom and nonuniform mating patterns and, as such, is in stark contrast to the approach used by artificial breeding programs.

In many species individuals do not mate randomly, but instead compete intensely for access to mates or are highly selective before accepting a potential mate (Andersson 1994). For example, male dominance in territorial contests is often an important determinant of breeding success, and, as a consequence, males of many species invest heavily into growth or other armaments that increase their success in such contests (Clutton-Brock 1982; Weckerly 1998). Alternatively, when members of one sex, typically females, are selective in which individuals they accept as mates, they can obtain direct benefits in resource-based mating systems (i.e., parental care or protection from predators) or indirect benefits (i.e., good or compatible genes) from their mate (review in Neff and Pitcher 2005). For example, females in some species are congruent in their mate choice for males that have an elaborate secondary sexual character such as a large ornament or bright colouration. Such congruent choice is typically for additive genetic benefits from good genes that the elaborate character “advertises” in the male (see Rowe and Houle 1996; Neff and Pitcher 2005). Alternatively, in other species, females are incongruent in their mating preferences and instead prefer different males. In a number of taxa, including salmonids and other fishes, this variation in preference has been linked to MHC diversity with females preferring MHC dissimilar males (e.g., Landry et al. 2001; Reusch et al. 2001; Garner et al. 2010). Increased MHC diversity in the offspring has been shown to increase pathogen resistance and survivorship of the offspring and thereby represents a nonadditive genetic benefit through compatible genes (e.g., Reusch et al. 2001).

To quantify the overall fitness benefits arising from mate choice, a number of studies have compared the offspring of individuals that mated with a preferred mate with the offspring of individuals that mated with a nonpreferred mate (Table 2). For example, female *Drosophila pseudoobscura* were allowed to select between two males in a mate choice arena and were then either mated to the preferred or nonpreferred male (Anderson et al. 2007). The number of offspring that survived to eclosion was about 20% higher for females that were paired with a preferred male than for females paired with a nonpreferred male. Similar results were found when

males were instead allowed to select between pairs of females. Another study in guppies (*Poecilia reticulata*), which used a similar design, found that preferred males sired offspring that were about 3% larger at birth than the offspring of nonpreferred males (von Ompteda 2003). Larger body size, especially early in life, can have large effects on survivorship in fish (Miller et al. 1988; Neff 2004b). No similar study, however, has been conducted on salmon. Nevertheless, across a range of taxa, sexual selection has been linked to a 36% median increase in fitness-related traits in the offspring (Table 2; but also see Møller and Alatalo 1999). Furthermore, mate choice can contribute to reproductive isolation between ecologically distinct groups of fish and thus helps preserve local adaptations to unique habitats (Hendry et al. 2000; Rundle et al. 2000).

Although sexual selection is often studied to understand patterns of natural diversity, there is an increasing awareness that sexual selection may be relevant to artificial breeding programs and managing captive populations (Wedekind 2002; Pitcher and Neff 2007). Artificially propagated animals typically experience little or no sexual selection, and when breeding pairs are chosen by managers, mate choice and male–male competition are excluded entirely. Many artificial breeding programs aim to maximize genetic diversity by ensuring that all individuals reproduce, which contrasts with natural breeding systems in which variance in reproductive success among individuals is typically high and that variance is often associated with the fitness of the offspring (Wedekind 2002; Quinn 2005). By allowing low-quality individuals to reproduce, or by mating individuals that are not genetically compatible, artificial breeding programs may actually facilitate the accumulation of maladaptive alleles and genotypes that might otherwise be purged by sexual selection (Quader 2005).

Only a few studies in fishes have critically evaluated the performance of offspring produced by natural mating with those produced by artificial mating through their entire life cycle. Consuegra and Garcia de Leaniz (2008) examined the linkage between mate choice, MHC variation, and offspring fitness in a natural population of Atlantic salmon. The authors compared MHC diversity and internal parasite prevalence among anadromous Atlantic salmon returning to rivers to spawn that had originated from natural spawning, where parents were allowed to mate freely, or artificial crosses. They found that offspring from artificially bred salmon had higher parasite loads and were four times more likely to be infected than salmon originated from parents that were allowed to mate freely. The authors attributed this difference to the fact that the naturally bred fish were more MHC dissimilar than would be expected by chance. In a second study, Agbali et al. (2010) used the Chinese rose bitterling (*Rhodeus ocellatus*) to examine the additive and nonadditive genetic benefits of mate choice. The authors first used a factorial breeding design and tracked the offspring through to sexual maturity and found a significant nonadditive genetic component to the genetic architecture of fitness that accounted for 36% of the variance in survival and 30% of the variance in growth rate. They then examined female mate choice and compared the performance of offspring from matings with preferred and nonpreferred males. Female mating preferences captured a significant portion of the nonadditive

Table 2. Experimental demonstrations of the benefits associated with natural mating.

Method of comparison	Species	Fitness measure	Effect size (%)	Reference
Sexual selection: female choice				
Preferred vs. nonpreferred	House mice (<i>Mus musculus</i>)	Offspring survival in field enclosures (60 days)	72%	Drickamer et al. 2000
	Guppy (<i>Poecilia reticulata</i>)	Dominance of male offspring	133%	Drickamer et al. 2003
Offspring size at birth		2.7%	von Ompteda 2003	
Choice vs. random mating	Pacific blue-eye (<i>Pseudomugil signifer</i>)	Offspring condition and critical swim speed	NS	Nicoletto 1995
		Offspring hatching success	547%	Wong 2004
	Deep-snouted pipefish (<i>Syngnathus typhle</i>)	Offspring survival following predator exposure	57%	Sandvik et al. 2000
		Offspring growth rate	36%	Sandvik et al. 2000
<i>Drosophila pseudoobscura</i>	Number of offspring surviving to eclosion	20%	Anderson et al. 2007	
Preferred vs. nonpreferred	House mice (<i>Mus musculus</i>)	Offspring nest quality in field enclosures	23%	Gowaty et al. 2003
		Dominance of male offspring	50%	Drickamer et al. 2003
	Deep-snouted pipefish (<i>Syngnathus typhle</i>)	Offspring survival following predator exposure	42%	Sandvik et al. 2000
Sexual selection: male choice	<i>Drosophila pseudoobscura</i>	Number of offspring surviving to eclosion	17%	Anderson et al. 2007
		Sexual selection: male competition		
Dominant vs. subordinate	Bank voles (<i>Myodes glareolus</i>)	Offspring survival to weaning	40%	Kruczek and Zatorska 2008
	Pacific blue-eye (<i>Pseudomugil signifer</i>)	Offspring hatching success	NS	Wong 2004
		Brown trout (<i>Salmo trutta</i>)	Offspring hatching success and survival	NS
	Rose bitterling (<i>Rhodeus ocellatus</i>)	Offspring survival	NS	Casalini et al. 2009

Note: Effect size was calculated as high/low – 1 and is expressed as a percentage. The effect of mate choice was assessed by comparing offspring produced by preferred and nonpreferred individuals, whereas the effect of competition for mates was assessed by comparing offspring produced by dominant and subordinate individuals. Pacific blue-eye breeding system is characterized by male-only parental care; female choice is presumably for parental care. Included are the mechanisms of sexual selection (mate choice or intrasexual competition), method of comparison, species, fitness measure, effect size, and the source reference.

effects on fitness and offspring from preferred matings outperformed those from matings with nonpreferred males. Agbali and colleagues (2010) also implicated the MHC as part of the nonadditive genetic effect because they found that females preferred males that were dissimilar from them at the MHC.

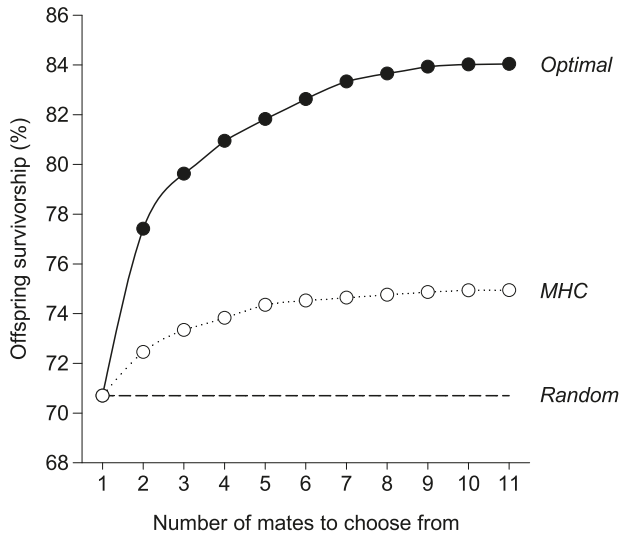
The potential for mate choice to make an impact on the genetic quality of offspring produced from artificial breeding programs has also been assessed using a modelling approach. These models typically use a full factorial breeding design to detail the components of the genetic architecture of fitness and then assess the potential increase in offspring genetic quality from optimal mating (i.e., maximize familial fitness for each female), optimal mating based on a single candidate fitness locus such as the MHC, and random mating. For example, Pitcher and Neff (2007) modelled the value of incorporating genetic quality into supportive breeding programs for Chinook salmon through increases in offspring survivor-

ship. Their model revealed that females that selected optimal males would increase their offspring survivorship by 19% during just the endogenous feeding period as compared with random mating (Fig. 3). Additionally, even if optimal mating was based only on a single fitness locus, the MHC class II, offspring fitness could be increased by 6% (also see Pitcher and Neff 2006). These modelling studies, in conjunction with empirical data showing that females do discriminate among males based on genetic quality, show the potential for incorporating natural mating into supportive breeding programs.

Recommendations for the management of wild fish populations

In the text below, we make hierarchical recommendations for the effective management and conservation of wild fish populations. We believe that each subsequent recommendation will be less effective at maintaining healthy wild popula-

Fig. 3. Model demonstrating the potential increase in offspring survivorship from mate choice in Chinook salmon (*Oncorhynchus tshawytscha*). The Random line represents the expected (average) offspring survivorship through to the end of the endogenous feeding period for females randomly mated to a single male. The MHC line and data points represent the potential benefit to selecting among up to 11 males optimally based on MHC genotype. The Optimal line and data points represent the potential benefit to selecting among up to 11 males optimally based on overall survivorship. The figure was redrawn from data presented in Pitcher and Neff (2007).



tions, but may be required when competing demands for ecosystem services are considered. In all cases, these recommendations should be implemented with the target of preserving existing populations in their native habitat to avoid the potential loss of local adaptations.

1. Rehabilitate and maintain healthy habitat and ecological function. Quinn (2005, p. 1491) wrote about salmon conservation, "No hatchery manager, regardless of the guidelines that he or she is given, can reproduce the patterns of breeding and selection that would occur in the stream." We share the concern of Quinn and others (e.g., Meffe 1992; Waples et al. 2007; Fraser 2008) that anthropogenic attempts to breed fish via artificial breeding programs are destined to produce individuals that are not well adapted to their local environments. Maintaining healthy habitats and ecological processes (e.g., sexual and natural selection) is the only effective approach to ensure the persistence of wild populations. Sexual selection can have enormous effects on mating patterns and can promote genetic quality in offspring. Competition for mating opportunities can improve genetic quality by preventing individuals that have genes associated with poor condition from reproducing, and facilitating mate choice can promote both good genes and compatible gene combinations. In systems where viable spawning habitat remains, the goal of the management program should be to ensure that a large and representative group of mature fish reach the breeding grounds. Constructing artificial breeding habitats may likewise facilitate sexual selection and its associated benefits in

areas where natural breeding habitats are limited. Such artificial habitats, however, should retain as much of the natural environment as possible, including, for example, exposure to water from the native stream including the natural pathogen community, natural food and prey items for the fry once they emerge, and some level of predation.

2. Incorporate natural ecological processes into artificial breeding programs. When augmented breeding is required, for example, because of the lack of healthy habitats or very low population sizes, incorporate as many aspects of natural ecological processes as possible. Sexual selection could be incorporated into breeding programs by facilitating mate choice and male–male competition. For example, mating preferences might be incorporated into artificial breeding schemes by allowing females to select from multiple males in a choice arena, as is routinely done in mating system research. The female and selected male could then be spawned following conventional hatchery procedures. Seminatual spawning channels have been used to breed salmon for scientific and sometimes commercial interests and can facilitate both male–male competition and mate choice. Alternatively, anthropogenic mate selection could target phenotypic traits including behaviours that are known to be subject to sexual selection with the premise that those traits are associated with genetic aspects of quality. Features of natural selection such as disease challenges and predation should be incorporated to some degree to minimize or counter selection imposed by the artificial hatchery environment and to promote genes associated with local adaptation to the natural environment.
3. Use a full or partial factorial breeding design in artificial breeding programs. When spawning habitat is compromised and seminatural habitat is inaccessible or logistically infeasible, implementing a full or partial factorial breeding design can maximize the number of genetic lineages produced and provide a wide target for natural and sexual selection to operate. To that end, the families should be maintained in the artificial environment for the minimal amount of time, and consideration of equalizing family sizes immediately prior to release into the natural environment should be considered. Equalization may help to reduce unintended selection imposed within the artificial environment. Additionally, when known, aspects of the genetic architecture of fitness could be incorporated into the breeding program. Additive genetic effects (good genes) sometimes can be identified phenotypically via condition-dependent traits. The advent of next-generation sequencing enables a wealth of genetic data to be generated even in nonmodel species, which considerably increases the capacity to identify genetic variation that contributes to adaptation (Stapley et al. 2010).

In all the cases noted above, broodstock should always come from the population targeted for management. When the target population has been extirpated, broodstock should come from another population that has a similar genetic architecture of fitness or, given that the architecture generally is unknown, from an ecologically similar population.

Conclusions

We have argued that there is little scientific evidence that artificial breeding programs meet their objective of rehabilitating or enhancing wild populations. We feel that the failure of these programs stems in part from a lack of appreciation for the complexity of the genetic architecture of fitness. Outside of small populations that suffer from strong inbreeding depression, programs that focus solely on maintaining genetic diversity may be less effective than those that also include consideration of the genetic architecture of fitness. Broad generalizations about the genetic architecture of fitness, such as maintaining genetic diversity via indices of multilocus heterozygosity, are too simplistic to be effective and should be abandoned. The evidence from natural populations indicates that outside of inbreeding depression in small populations, multilocus heterozygosity does not contribute to fitness. Even temporal monitoring of neutral diversity at a small number of loci is unlikely to provide insight into population demography that is not already available from hatchery breeding records and natural abundance surveys. Maintaining genetic diversity to allow populations to evolve in response to changing environments is theoretically plausible, but it is not yet supported empirically. More research is needed in this area before any meaningful recommendation can be made about the importance of genetic diversity for the evolvability of populations and future adaptation in fishes and how best to measure such diversity to maximize evolvability. Ultimately, artificial breeding programs should only be considered as a short-term solution to the management of populations that are in imminent peril of extirpation. Effective management otherwise should take a broader ecosystem approach and focus on maintaining healthy habitats and natural ecological processes. More generally, it has become apparent that the world fisheries are fully taxed and cannot meet any further increase in global demand for fish products. Such demand must instead be diverted to alternative sources including aquaculture. Indeed, of the four major sources of animal protein for human consumption, comprising chicken, pork, beef, and fish, only fish are not yet domesticated and widely farmed.

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Appendix A. Glossary of terms

Artificial breeding programs — the planned breeding of organisms in captivity for the purpose of conservation or production.

Captive breeding — the bringing into captivity a large proportion of a critically endangered population to rear subsequent generations for eventual re-release into the wild.

Compatible genes — alleles whose effects on fitness depend on the genetic architecture at the rest of the genome and thereby show nonadditive effects.

Ecosystem services — the total direct (i.e., harvest opportunities) and indirect benefits (i.e., biodiversity conservation) provided by an ecosystem.

Epistasis — genes whose effects are modified by the genotype at one or more other loci.

Evolvability — the ability of a population to exploit existing genetic variation to respond to natural selection. Broader

definitions also include the ability of the population to generate genetic variation, albeit in this review we focus on the first part of the definition.

Fitness — the number of copies of its genes that an individual contributes to the next generation. Typically measured as lifetime reproductive success.

Gene pool — all of the alleles present in a population.

Genetic architecture of fitness — the underlying genetic basis of fitness or fitness-related traits.

Good genes — alleles that increase fitness independent of an individual's genetic architecture at the rest of the genome and thereby show additive effects.

Identity disequilibrium — a nonrandom association of alleles at two or more loci. Not necessarily caused by physical linkage of loci on the same chromosome, but can for example arise when inbreeding leads to loss of heterozygosity at both marker loci as well as the rest of the genome.

Inbreeding depression — negative effects of inbreeding on fitness that typically arises because inbreeding exposes deleterious recessive alleles to selection or because of reduced heterozygosity and the loss of benefits from overdominance.

Local adaptation — alleles that increase fitness in one location, but not in other locations within the habitable range of the species.

Mate choice — nonrandom mating arising from a preference by one sex (usually females) for specific characteristics when selecting mates.

Narrow-sense heritability — proportion of the total phenotypic variation within a population that is explained by additive genetic variation.

Natural selection — a difference in survival or reproductive success arising from phenotypic differences among individuals. When phenotypic differences are heritable, these fitness differences can lead to evolution.

Next-generation sequencing — simultaneous sequencing of multiple target DNA sequences providing upwards of millions of sequence reads in a single run.

Overdominance — a heterozygote advantage in which individuals that are heterozygous at a locus have higher fitness than individuals who are homozygous for either of the alleles present in the heterozygous individual.

Secondary sexual character — a sexually dimorphic characteristic that is not part of the reproductive system. Typically involved in sexual selection through effects on mate choice or competition for mates.

Sexual selection — selection arising from differences in mating success among individuals within a population. Typically arises either from mate choice or from competition within a sex for mating opportunities.

Sperm competition — competition between the sperm of two or more males to fertilize an ovum.

Standing genetic variation — the presence of multiple alleles at a locus within a population.

Supportive breeding — bringing into captivity a small fraction of individuals from the wild for reproduction and then returning their offspring into their native habitat.