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Interbreeding of genetically distinct native brown trout (*Salmo trutta*) populations designates offspring fitness

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ABSTRACT

Supportive breeding with subsequent stocking is an important long-term conservation tool for sustaining harvestable populations and genetic diversity in wild fish populations. In salmonids, this strategy often implies, inadvertently or for logistic reasons, breeding of a mixture of local populations, which may lead to loss of local adaptation and pose risks to receiving populations. In an alpine lake system in Norway (Pålsbu-Tunhovd), we assessed long-term effects of interbreeding three brown trout (*Salmo trutta*) populations from separate and environmentally contrasting spawning and recruitment habitats. Using a Bayesian genetic assignment algorithm we compared numeric contributions and genetic and demographic characteristics of wild-born and lake-stocked fish within and across populations. Population contribution by the broodstock was disproportional to the number of surviving and reproductively ready stocked brown trout, indicating higher lifetime survival for brown trout descending from a large river dominated by large fish. Life history selection was further indicated by a discrepancy between observed and expected numbers of adult hybrids, i.e., fewer hybrids suggest negative fitness effects of hybridization. Hence, supportive breeding changed gene frequencies, although reduced genetic variation was not documented in mature stocked brown trout. Post stocking, these fish retained the initial length advantage relative to the fastest-growing wild-born population until the age of ten. Stocked brown trout had similar growth rates regardless of genetic origin, whereas wild-born brown trout growth rates differed among recruitment habitats. Our study in this system indicates that genetic origin determined longevity. Genetics may be a less important determinant for growth rates in lake-stocked than in wild-born brown trout.

1. Introduction

Sustaining genetic diversity within and among populations is a primary goal of species conservation and management (Caballero et al., 2010). Population structure, interbreeding of populations and within-population genetic variation affect evolutionary potential (Fisher, 1930), and loss of genetic diversity often is associated with population and individual fitness decrease (Bouzat, 2010). Environmental variation also may influence fitness variation, in particular on local scales, for example in fish (Cena et al., 2006).

In salmonids, anthropogenic habitat fragmentation and destruction is considered the single most important factor responsible for biodiversity loss (DiBattista, 2008; Lovejoy, 1996), and impounding dams often lead to reduced viability of wild populations (Morita et al., 2009). Stocking of salmonid fish is therefore a widespread management strategy, mainly to sustain sport fishing and commercial harvest, but also to support wild populations. These objectives may not, however, be compatible; maximizing stocked fish survival for harvest does not necessarily sustain the integrity of wild populations (Fraser, 2008). Unfortunately, risk assessment-based conservation approaches are infrequently implemented (Cowx and Gerdeaux, 2004; Cowx et al., 2010). The potential long-term consequences of stocking depend both on genetic and demographic characteristics of stocked fish and their lifetime fitness (Mehner et al., 2009). Despite efforts to optimize biodiversity in captive breeding programs (Fraser, 2008; Wang et al., 2002), reduced genetic variation may arise in populations of reared fish, resulting from small effective population sizes of the bred parental stock (i.e., the broodstock), artificial and natural selection, or differential reproductive success (Fraser, 2008; Ryman and Laikre, 1991). Furthermore, cultured fish often diverge from their wild relatives, genetically and phenotypically (Araki and Schmid, 2010; Jonsson and Jonsson, 2006), also as a result of adaptation to artificial environments (domestication selection). For example, hatchery practices promoting rapid juvenile growth often result in younger age at maturity and decreased longevity (Jonsson and Jonsson, 2006). Subsequent generations of stocked salmonids with a history of captive breeding may generally

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have reduced fitness, although evidence mainly exists from steelhead (*Oncorhynchus mykiss*) (Araki et al., 2008). Models indicate a possible fitness reduction of wild-born descendants from stocked fish of >50% per generation, and empirical studies have similarly shown fitness declines of >30% per generation, likely due to domestication selection (Araki et al., 2008). On the other hand, cultured and released individuals can influence the genetic composition (e.g., allelic composition, diversity and gene expression) of wild populations through competition and interbreeding (Frankham, 2008; Fraser et al., 2008; Marie et al., 2010).

Supportive breeding program, involving catch of local broodstock annually to increase survival of offspring (Ryman and Laikre, 1991), are implemented to minimize potential negative effects of stocking on wild fish (Ford, 2002; Small et al., 2009). However, small natural populations with few spawners, combined with limited fieldwork resources and limited knowledge of genetic structure within local catchment areas (e.g., lake ecosystems), have led, intended or not, to mixture of broodstock and hybridization among genetically differentiated local strains in such breeding programs (i.e., semi-supportive breeding, Wollebaek et al., 2010). Furthermore, many hatchery operations apply mixed-milt fertilization to ease the production and to increase genetic variation and fertilization success. There may be a risk, however, of unintended increased variance in individual fertilization success that may reduce the effective population size (Campton, 2004; Kekalainen et al., 2010; Ottesen et al., 2009; Wedekind et al., 2007). However, even though deliberate mating schemes (e.g., factorial mating) can approximate natural selection mechanisms (Campton, 2004; Eldridge and Killebrew, 2008; Neff et al., 2011), stocking-based management cannot match natural reproduction processes (i.e., mate selection and adaptation).

Fitness of young offspring from interbreeding of closely related populations (i.e., admixture) often increases in the first generation, as opposed to their subsequent generations, e.g., due to disruption of local adaptation, underdominance or epistatic interactions (Edmands, 2007). Hatchery selection may lead to loss of genetic diversity and induce artificial selection for specific life-history traits (Campton, 2004), potentially maladaptive in the wild after stocking. Outbreeding experiments in salmonids tend to suggest positive fitness effects for population hybrids in captivity, but not always in the wild, although results are ambiguous (McClelland and Naish, 2007). Thus, prediction of the long-term genetic consequences of supportive breeding is a challenge, but it is crucial (Duchesne and Bernatchez, 2002). In spite of its obvious importance, this kind of research has not attracted much attention. The few existing salmonid studies that address fitness of spatially or temporally segregated populations bred in admixture (Gharrett et al., 1999; Gilk et al., 2004) focused on early life-stage survival (Fraser et al., 2011), as opposed to long-term survival. There is an urgent need for natural experiments of adult hybrid fitness in their parental environments. Linking genetic contribution to demographic differentiation of populations would shed light on long-term effects of supportive breeding, and highlight potential impacts of conservation and fishery management programs.

Brown trout (*Salmo trutta*) exhibit indeterminate growth and longevity increases with latitude (Blanck and Lamouroux, 2007; Jonsson and L'Abée-Lund, 1993; Jonsson et al., 1991) and colder climate (McDermid et al., 2010). Northern alpine populations are thus suitable for comparative studies of stocked brown trout fitness, using growth and longevity as proxies for fitness (Roff and Mousseau, 1987). In this study, we compare fitness of stocked brown trout from semi-supportive breeding (where admixed wild and previously stocked fish are included in the annual broodstock) with their wild-born counterparts within and among populations. The main objective was to quantify to which degree genetic population contributions in admixed breeding reflect long-term survival of stocked brown trout. Potential conformity between parental environments and fitness was assessed by population-level comparisons of genetic diversity, growth and survival, and longevity fitness.

2. Material and methods

2.1. Study sites

Lake Pålsbufjord (PAL) and Lake Tunhovdfjord (TUN), separated by a dam established in 1946 with fishways that maintain migration between the lakes, have six potential spawning and recruitment stream habitats for brown trout (Fig. 1). Water flow and habitat area vary considerably across sites (Appendix 1). In total, about 1 million brown trout have been lake-stocked since the late 1950s. Until 1998, brown trout of different origins, age groups (0+ to 6 years) and numbers (0 to 51 500) were stocked annually. Since 1999, about 3000 and 10 000 adipose fin-clipped yearlings have been stocked annually in PAL and TUN, respectively. Stocked, i.e., fin-clipped, brown trout typically make up 10–45% of annual adult fish catches (Aass, 1990; Brabrand et al., 2008; L'Abée-Lund et al., 2002). However, stocked brown trout do not ascend the recruitment streams to spawn, and genetic introgression due to stocking is unlikely (Wollebaek et al., 2010).

2.2. Supportive breeding

In a semi-supportive breeding program, implemented since 1970, brown trout are caught annually in Lake TUN prior to and during spawning migration in October, for breeding in November. Only larger fish (>35 cm total length) have been included in the broodstock as these individuals were thought to be piscivorous and genetically adapted to fast growth (Aass, 1973), but without any consideration of local genetic origin or life history variation. Recent studies have confirmed that brown trout from all stream habitats in both lakes have been represented in the annually and randomly captured broodstock (Brabrand et al., 2008). The numbers of breeders in these samples were typically 70–120 fish, of which ca. 70% were females. Wild-born and previously stocked first-generation (F_1) hatchery-born brown trout (adipose fin-clipped) were included in the broodstock. The breeding scheme did not consider any selection criteria other than size. Overlapping pairwise spawning, where multiple males (ca. 3–4) were mated with a single female (Campton, 2004), was implemented without consideration of family size. Stripped sperm samples were activated at the same time to avoid sperm competition. Common containers were used for all individuals, from sperm activation of eggs through hatchery breeding, to stocking as yearlings at multiple locations along the shores in both lakes. Thus, we did not expect fitness variation between family groups or populations due to variation in hatchery conditions.

2.3. Sampling

During 2006 to 2008, fin-clips were taken from all ripe (i.e., sexually mature) brown trout included in the broodstock ($n = 323$), on average 108 brown trout (SD ± 29, range 75–129) annually, mean 35 males (SD ± 8, range 26–42) and 73 females (SD ± 29, range 49–87). This broodstock sample (B) included wild-born (W) and first-generation (F_1) stocked (S, adipose fin-clipped) brown trout. Fish used as broodstock consisted of more than 10 year-classes (as determined from scale analyses). This practice reduced the potential sampling bias, e.g., due to overrepresentation of single males in siring young because of potential bias in sperm competition. Sample B was assumed to be representative of broodstock also for previously stocked fish (S). Historical genetic samples were unavailable. Total lengths (L_T) of ripe brown trout were measured and sex determined during spawning. Individual ages were determined by scale analyses, followed by back-calculation of age to estimate annual growth (L_A), assuming proportionality among fish length and age structure (Lea, 1910). Previous samples of non-ripe, wild-born brown trout collected from the six spawning habitats in the lakes in 2005–2007 ($n = 226$, 30–40 per site, Wollebaek et al., submitted) were included to assist inference of the genetic population structure.