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Parental characteristics versus egg survival: towards an improved genetic management in the supportive breeding of lake whitefish

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A number of sexual selection models predict that reproductive success in the wild is positively linked to heritable viability (e.g. the "good genes" models). Here we explore whether there is information about heritable viability that could potentially be used in the hatchery management of Alpine lake whitefish (*Coregonus* sp.). We drew 20 wild-caught individuals out of a breeding program, crossed them in a fully balanced 10 females × 10 males mating design, and incubated each sibship in several replicates until hatching. We then compared egg survival with parental characteristics. Egg number or milt volume were not significantly correlated with egg survival, nor was egg size. However, female size and age, and male quality indicators such as condition factor, breeding ornamentation, and fluctuating asymmetry, were useful predictors of egg survival. We discuss the possibility that a promotion of heritable viability could be carefully balanced with the maintenance of genetic variation in order to maximize the survival prospects of a population.

Introduction

Lake whitefish (*Coregonus* sp.) are among the fish species that are routinely caught during the breeding season and stripped for their gametes. The resulting fertilized eggs are reared until hatching when the offspring are released into the wild. Usually, such supportive breeding programs increase or at least help to maintain population size in terms of absolute numbers. However, there are a number of risks involved in supportive breeding, especially if the potential impact of such programs on the genetics of a population is not given enough consideration (Frankham 1995, Lande 1998). In the following discussion of the possible consequences of supportive breeding we will therefore use an important concept in population genetics, namely the effective population number N_e. N_e gives the size of an "ideal" population that loses genetic variation at the same rate as the actual population (Wright 1969, Hartl 1988). Estimation of N_e can be complicated (e.g. Rieman & Allendorf 2001, Waples 2002b, 2002a), but a generally valid rule is that N_e is usually well below the census size N_c.

Dividing a population into captive-breeding and wild-breeding components normally reduces N_e because it increases the variance in reproductive success in the total population (Ryman & Laikre 1991, Wang & Caballero 1999, Wang & Ryman 2001, but *see* also Duchesne & Bernatchez 2002). Increased variance in reproductive success means increased inbreeding and hence an increased loss of heterozygosity and of genetic variation. These are relevant issues even for populations that are not endangered (Frankham 1995). A supportive breeding program that does not result in a substantial and continuous increase of the census size of the breeding population can be considered as genetically harmful because of elevated rates of inbreeding and genetic drift (Wang & Ryman 2001). In reaction to these genetic risks, the breeding regime followed in hatcheries usually aims at keeping the variance in individual reproductive success low (Wang & Hill 2000). Furthermore, the captive-bred subpopulations are ideally kept above a certain minimal number. Ryman *et al.* (1999) suggested, as a rule of thumb, an N_e within the captive (parental) population of at least 50.

A further potential problem of supportive breeding is the fact that it usually circumvents potential mate choice decisions (Wedekind 2002a), whereas in nature individuals normally compete for access to mating partners and they choose their mates (Andersson 1994). Circumventing sexual selection could have negative consequences for the genetics of a population, especially where N_e has not yet become very small, because intra- and intersexual conflicts are expected to select against deleterious mutations. Furthermore, a number of so called “good genes models” predict that sexual selection enhances mean resistance to pathogens in a population (reviews in Grahn *et al.* 1998, Westneat & Birkhead 1998, Møller & Alatalo 1999, Jennions & Petrie 2000).

Supportive breeding should certainly minimize variance in reproductive success that is not linked to viability traits in order to keep the loss of genetic variation small. However, the viability of fish embryos and larvae can vary dramatically (Bromage *et al.* 1992, Nagler *et al.* 2000, Wedekind *et al.* 2001). If some of this variance is due to heritable viability, minimizing the variance in reproductive success and thereby maximizing N_e might not be the best population management strategy. If a reproductive skew, i.e. the variance in reproductive success, can be linked to viability indicators, there might be a way to optimize this skew with respect to later recruitment rates and with respect to the survival prospects of a population (Wedekind 2002a).

Some whitefish populations in Switzerland are mainly if not exclusively maintained by supportive breeding because of recent eutrophication and consequent oxygen problems for naturally spawned eggs (Ventling-Schwank & Müller 1991). Wedekind *et al.* (2001) found in one of these populations that parents differ significantly with respect to the survival of their offspring: egg survival until hatching was strongly influenced by maternal, paternal, and maternal–paternal interaction effects. Here, we use these egg mortality data and compare them to parental characteristics and various breeding options in the hatchery.

The present study has the following aims: first, we use the reproductive output (egg counts and milt volume) of the 20 parental fish that had been stripped in the course of our previous study (Wedekind *et al.* 2001) in order to discuss various breeding regimes in the hatchery with respect to the anticipated loss of heterozygosity (as a measure of genetic variation). The breeding regimes we discuss here are: (i) randomly mixing all available gametes (i.e. the individual reproductive success is correlated with the number of gametes stripped), (ii) equalizing male success (e.g. by using fixed amounts of milt or by fertilizing equal amounts of eggs per male), and (iii) equalizing male and female success (i.e. using equal numbers of eggs per female and discarding the remaining eggs). Second, we test whether the number of eggs or the amount of milt we could strip from the fish are correlated with egg survival, i.e. whether equalizing the reproductive success in the hatchery influences the average egg mortality. Third, we test whether egg size is correlated with egg survival in our experimental situation. Fourth, we use a number of potential quality indicators, such as size, age, condition factor, breeding ornamentation, and fluctuating asymmetry of the parental fish, to explore whether egg survival could partly be predicted by parental characteristics. Finally, we use the mortality data of our previous study (Wedekind *et al.* 2001) to discuss whether there might be, in principle, a way to optimize the maintenance of genetic variation and the promotion of heritable viability in order to maximize the long-term survival prospects of a population.

Methods

The whitefish we studied were a sample drawn out of a breeding program in a hatchery at Lake Hallwil in the central Swiss lowland (surface area: 10.2 km^2, mean depth: 28.6 m, eutrophic). We sampled in mid-December, i.e. during the breeding season of the population. The fish had been caught with a gill net from their spawning place and brought alive to the hatchery where we randomly selected ten males and ten females and used them for stripping. The gametes of each fish were collected separately in a Petri dish. We used all the eggs of the females and 100 μl of milt per male for controlled fertilizations (*see* methods below). The remaining milt was weighed to the nearest 0.01 g. As the fertilized eggs were afterwards reared under controlled conditions in family groups, egg number per female could be determined later before hatching.

We measured the parental fish standard length (excluding tail fin) to the nearest mm, and total body weight and the remaining weight of the gonads to the nearest 0.1 g. The weight of the gonads and any gut content was subtracted from the total body weight in order to get a "net body weight" that was meant to correct for potential differences in gut content and in the remaining gonad size. Total body weight and "net body weight" was highly correlated (Pearson's r = 0.99, n = 20, $p << 0.001$). We nevertheless used net body weight for the statistical analyses (using total body weight would not change the results qualitatively). We estimated the age of the fish from the number of growth rings on scales taken from above the lateral line below the dorsal fin.

Condition factor is a useful indicator of a fish's general health and vigour at a given moment (Bolger & Connoly 1989). We calculated two types of condition factors. The first type is calculated with the formula ($k \times$ standard length)/(weight)^3, with $k = 10^5$. The second type is calculated for each sex with the formula ($k \times$ standard length)/(weight)^b, with $k = 10^5$ and b = the slope of the logarithmic regression of weight on standard length (Bolger & Connoly 1989) (males: $b = 3.79$, r^2 of the logarithmic regression = 0.89; females: $b = 3.08$, $r^2 = 0.94$; $n = 10$ each). As both types of condition factors lead to the same qualitative results, we present only the more commonly used one with the exponent = 3 for both sexes.

A potentially important phenotypic marker of condition is fluctuating asymmetry (FA). FA is non-directional deviation from perfect bilateral symmetry in traits that are, on average, bilaterally symmetrical. FA normally reflects the ability to deal with stress, both genetic and environmental, during ontogeny (Møller & Swaddle 1997). A number of studies on other species further conclude that individuals with relatively low FA experience greater mating success or attractiveness to the opposite sex (Møller & Thornhill 1998). We measured FA on the paired pelvic fins (= ventral fins) as the trait's absolute asymmetry divided by the mean trait size $\{|(\text{left} - \text{right})|/[(\text{left} + \text{right})/2]\}$. Therefore, the pelvic fins were carefully cut at their bases and spread on plastic transparencies where they were dried for several weeks. We then determined their dry weight to the nearest 0.1 mg. We did not use the pectoral fins for measuring asymmetry because they were damaged in some fish.

The breeding ornamentation of whitefish is typical for many teleost species and consists of breeding tubercles (Wiley & Collette 1970). In the case of our study species, both males and females develop this kind of breeding ornamentation. We made plaster casts of the right side of each male and female (*see* detailed methods in Wedekind 1992). We used the average cast depth of the largest 10 tubercles near the lateral line vertically above the anal fin as a measure of the breeding ornamentation (the breeding ornamentation of some of the fish was obviously damaged at other places due to abrasions from the gill nets). The cast depths were measured with a Digimatic Indicator 0.001–50 mm (Mitutoyo).

In order to study offspring performance with respect to parental origin, each female's

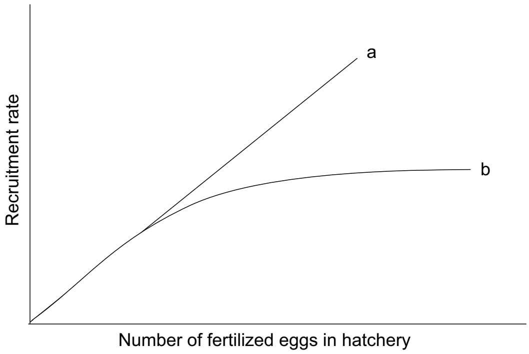

Fig. 1. The number of fertilized eggs in a hatchery is unlikely to correspond linearily (line a) to later recruitment rates. Habitat limitations and other factors may instead lead to an asymptotic curve like, for example, line b. As a consequence, female reproductive success can often be equalized in the hatchery (i.e. surplus eggs discarded) without much effect on later recruitment rates.

freshly stripped eggs were about equally distributed to ten new Petri dishes. Each of these ten subsamples were then fertilized by adding 10 μl of one of the ten males' milt and adding some lake water. In this way we produced 100 different sibships (10 females × 10 males). The eggs of each sibship were then distributed to five new Petri dishes (diameter = 9 cm, water level = about 1 cm, no cover) and from then on kept in a climate room at constant 8 °C with regular water exchange every two weeks for the first 30 days, and once every week from then on. Care was taken to randomize the position of each Petri dish in the climate room (we used a blockwise randomization procedure). At least once per week we removed dead or obviously infected eggs and recorded their number.

Egg diameter was determined eight days after fertilization. We used a random sampling procedure to pick out 10 eggs per female. We determined the egg diameter under a microscope to the nearest 0.01 mm. All measured eggs appeared to be healthy and containing a normally-developing embryo each.

One of the five egg batches per sibship (i.e. 100 in total) was used in the course of another study (Wedekind 2002b). The remaining 400 egg batches were used to record the cumulative egg mortalities between day 0 and day 30 ("early mortality"), and between day 30 and hatching (which was expected to take place around day 60; Ventling-Schwank & Müller 1991). This "late mortality" was connected to an uncontrolled epidemic by *Pseudomonas fluorescens*, a virulent whitefish pathogen that was probably introduced into the system via one of the water exchanges (Wedekind *et al.* 2001, Wedekind 2002b). While late mortality was linked to the presence of the pathogen, regular examination under the microscope suggested that early mortality was mainly due to developmental problems. Indeed, early and late mortality were not correlated, i.e. they were different types of egg mortalities (Wedekind *et al.* 2001).

One could reduce the variance in reproductive success and hence the loss of genetic variation by using equal amounts of milt per male and equal amounts of eggs per female. Obviously, using equal amounts of eggs per female would result in a reduction of hatchlings as compared with using all eggs. However, such a reduction may not be significant if the recruitment rate is, from a certain minimal egg number on, more dependent on the wild environment's carrying capacity than on the number of fertilized eggs in the hatcheries (Fig. 1). In the following, we therefore include equalizing reproductive success in our discussion of potential breeding regimes in the hatcheries.

In order to get an impression about the effect of various breeding regimes on the loss of genetic variation in our sample, we assumed, for simplicity, a stable population size over time (i.e. on average two successful breeders among the offspring of each male or female) and random selection after fertilization. We then could use the formula

$$H_t = [1 - 1/(2N_e)]^t \times H_0 \tag{1}$$

to estimate the average heterozygosity at time t (H_t) as a measure of genetic variation, when t is the time in generations, and H_0 is the initial heterozygosity in the parental population (neutrality model of Wright 1969). The effective population size (N_e) was calculated at equal sex ratios as

$$N_e = (4N_c - 2)/(s^2 + 2) \tag{2}$$

(Wright 1969). In our case, the census size (N_c) is always 20, while s^2, i.e. the variance in reproductive success, had to be individually determined for each breeding regime. We therefore randomly assigned 20 offspring to the ten males and the ten females according to their expected breeding success, calculated the variance in the reproductive success among the parents, and repeated this procedure at least 500 times for each defined breeding regime. The average s^2 of all runs was then used in Eq. 2.

For unequal sex ratios, we used the formula

$$N_e = (4N_m N_f)/(N_m + N_f) \quad (3)$$

to calculate the effective population and hence the loss of genetic variation over time (Hartl 1988).

Results

Egg counts, milt volumes, and calculated loss of genetic variation

We found considerable variation among the ten males and the ten females in the amount of gametes that could be stripped (Table 1). If all gametes would be randomly mixed at fertilization, the variance in reproductive success and hence the loss of heterozygosity would be high as compared with when equalizing male success or male and female success (Fig. 2).

Egg counts and milt volumes versus egg survival

The average early mortality in the 400 egg batches was 10% (SE = 0.6%), while the average late mortality was 15% (SE = 1%). Total mortality was on average 23% (SE = 1%) (Table 2).

The sperm volume that could be stripped was not a significant predictor of early mortality ($r = -0.11$), late mortality ($r = -0.44$), nor total offspring mortality until hatching ($r = -0.49$, $n = 10$, p always > 0.15, two-tailed). Also, the number of eggs that could be stripped per female was not a significant predictor of any egg mortality measure (early mortality: $r = -0.23$, late mortality: $r = 0.46$, total mortality: $r < 0.01$, p always > 0.15). As a consequence, randomly mixing all

Table 1. Total number of eggs stripped, total milt volume stripped, condition factor, fluctuating asymmetry (FA), and the mean size of the largest ten breeding tubercles above the anal fin as a measure of breeding ornamentation of all females and males that were used as breeders in the study.

	Breeder	Number of eggs or milt volume (µl) stripped	Mean egg diameter (mm)	Condition	FA	Breeding tubercles (µm)
Female	#A	7611	2.17	1.10	0.04	156.8
	#B	4837	2.35	1.11	0.04	248.0
	#C	4235	2.35	1.03	0.13	45.6
	#D	8917	2.23	0.99	0.09	106.0
	#E	8283	2.26	1.18	0.11	48.7
	#F	4148	2.22	1.16	0.03	53.1
	#G	4726	2.10	1.15	0.02	140.7
	#H	9191	2.20	1.28	0.08	138.4
	#I	7822	2.17	1.07	0.02	152.9
	#K	10145	2.20	1.11	0.01	112.3
Male	#1	440		1.25	0.03	153.5
	#2	280		1.23	0.04	188.9
	#3	920		1.24	0.04	104.3
	#4	370		1.15	0.05	214.7
	#5	480		1.10	0.07	0
	#6	580		1.24	0.16	349.8
	#7	150		1.03	0.06	386.2
	#8	450		1.21	0.06	160.6
	#9	300		1.12	0.13	173.2
	#10	110		1.13	0.39	29.0

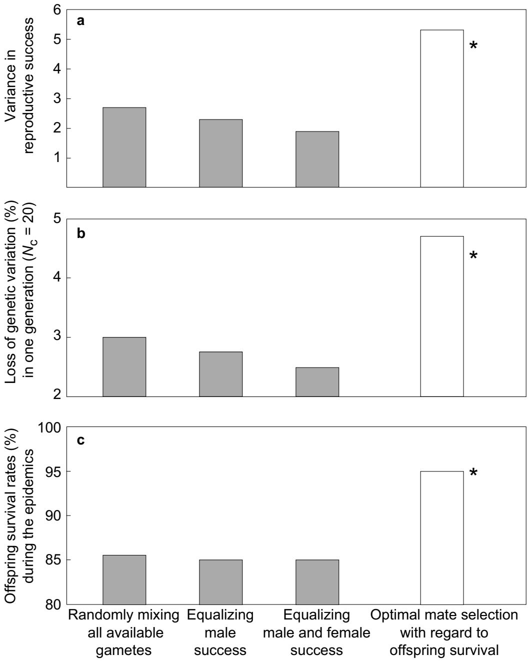

Fig. 2. The effects of different mating regimes on (**a**) the variance in reproductive success and (**b**) the loss of genetic variation in the next generation (here measured as the loss of heterozygosity at the moment of fertilization, assuming stable population size and random selection after fertilization). The experimental 10 × 10 mating design further allowed determining the survival rates of all possible types of offspring during an epidemic by *Pseudomonas fluorescens*. Panel **c** gives the calculated mean survival rates of the offspring that would result from the different breeding regimes, assuming that parasite pressure is constant. Grey bars indicate some options in the hatchery. Open bars indicate the theoretical potential of optimal mate selection as determined in Wedekind *et al.* (2001). Equalizing the females'reproductive success at optimal mate selection would reduce the variance in reproductive success and the loss of genetic variation to the levels indicated by the asterisks.

available gametes or equalizing male, or male and female, reproductive success would yield similar survival rates (Fig. 2c).

Egg survival versus egg size

Egg size differed among the females (ANOVA, $F = 12.7$, df = 9, $p < 0.001$). However, we could not find any correlations between egg size and any measure of egg mortality ($-0.24 < r < 0.11$, p always > 0.50). Egg size was also not correlated with the size or to potential quality indicators of the females (p always > 0.05).

Egg survival versus parental size, age and potential quality indicators

The age of the females ranged from 2+ to 6+ in our sample, while all males were 2+ except one that was 3+. Age, length and weight were all highly correlated (females: $r \geq 0.92$, p always < 0.001; length versus weight in males: $r = 0.95$, $p < 0.001$). Male size (or age) was not significantly linked to any kind of offspring mortality (early mortality versus fish length: $r = -0.13$, $n = 10$, $p = 0.72$; late mortality versus fish length: $r = -0.15$, $p = 0.67$). Female size (or age) was also not correlated with early mortality (early mortality versus female length: $r = 0.30$, $n = 10$, $p = 0.40$). However, female size was a significant predictor of late egg mortality (late mortality versus fish length: $r = 0.87$, $p = 0.001$), and female age was a significant predictor of both types of mortality (age versus early mortality: $r = 0.53$; $p = 0.016$, age versus late mortality: $r = 0.51$, $p = 0.02$). Older females had eggs that had a lower survival rate as compared with the surival rate of the eggs of younger females.

The three potential quality indicators (Table 1), i.e. condition factor, fluctuating asymmetry (FA), and size of breeding tubercles, did not correlate with one another (in females and in males: $-0.50 < r < 0.03$, p always > 0.4, directed).

Tables 3 and 4 show the results of multiple regressions of the three potential quality indicators on early and late egg mortality. In the females, these indicators did not correlate with any kind of egg mortality. In the males, however, all three indicators appeared to be useful predictors of late mortality, i.e. the offspring's susceptibility to an infection. These findings remain significant after using Bonferroni correction for multiple testing.

Trading offspring survival for loss of genetic variation

The average late egg mortalities ranged from 10.6% to 26.4% per male. As a consequence, if we had used only the very best male with respect to late egg mortality to fertilize all eggs (and all else being equal), the offspring survival during the epidemics would be 89.4%. However, the remaining genetic variance in the next generation would be very low due to unequal sex ratio and high variance in reproductive success. If we would equally use sperm of only the best two males (again with respect to late egg survival) to fertilize all females' eggs, we would save some more genetic variation in the next generation but reduce the average egg survival. Figure 3 gives the calculated egg survival rate during the epidemics and the remaining genetic variation in the next generation for all possible numbers of best males used.

The male with the largest breeding tubercles was the best male, while the worst two males

Table 2. Mortality of the 100 sibships (average of four replicates each).

Male	Female									
	#A	#B	#C	#D	#E	#F	#G	#H	#J	#K
Early mortality (%)										
#1	47.2	4.8	11.9	11.2	1.8	6.5	34.4	7.9	5.8	4.6
#2	34.3	4.0	14.6	3.5	3.2	9.9	19.3	5.3	0.4	2.2
#3	31.0	3.8	11.3	2.6	2.5	6.4	19.2	4.1	1.3	1.8
#4	34.0	3.6	13.1	2.9	2.3	3.2	15.8	3.3	2.3	2.9
#5	31.5	3.0	12.0	4.4	1.0	7.3	12.2	3.2	3.0	2.7
#6	47.8	4.3	26.7	3.4	2.3	2.5	14.2	3.1	1.9	2.4
#7	42.0	4.7	17.6	4.4	2.2	5.3	11.9	2.9	2.6	2.8
#8	36.7	2.3	21.7	2.0	1.9	9.9	19.8	3.2	1.3	2.3
#9	35.8	3.0	13.0	3.3	1.0	7.3	13.8	4.0	1.4	1.7
#10	50.7	4.7	14.9	2.5	2.2	8.6	10.5	2.6	2.3	2.6
Late mortality (%)										
#1	5.7	11.6	16.2	4.1	17.9	8.9	2.8	24.5	26.7	3.2
#2	7.1	10.9	6.7	4.3	30.9	6.2	5.7	21.9	5.0	12.5
#3	29.5	6.1	5.8	6.2	33.5	5.0	7.5	26.3	9.7	10.0
#4	19.7	20.8	12.5	3.9	13.8	7.1	7.8	21.4	28.9	12.9
#5	31.8	12.0	8.0	7.8	13.8	37.9	2.8	32.2	14.2	26.3
#6	15.8	15.5	19.1	1.6	11.7	3.7	2.2	22.5	4.5	9.9
#7	24.7	13.4	9.2	6.2	12.9	6.3	7.7	22.3	30.3	13.7
#8	13.7	23.0	21.2	1.1	2.8	9.9	1.3	19.3	12.5	6.1
#9	30.7	3.8	24.2	33.4	8.7	11.8	5.1	29.2	16.0	17.1
#10	40.3	38.7	5.8	43.3	28.4	14.8	13.5	38.1	27.5	14.3

Table 3. Multiple regression of potential *male* quality indicators on early egg mortality (global $F = 1.0$, df = 3, $p = 0.47$), and on late egg mortality (global $F = 41.1$, $p < 0.001$).

Potential quality indicator	Direction of the effect		F	p
	Expected	Observed		
Early mortality				
Condition factor	–	+	2.5	0.170
Breeding ornamentation	–	+	0.8	0.410
Fluctuating asymmetry	+	+	0.4	0.540
Late mortality				
Condition factor	–	–	26.8	0.002
Breeding ornamentation	–	–	24.8	0.003
Fluctuating asymmetry	+	+	36.2	0.001

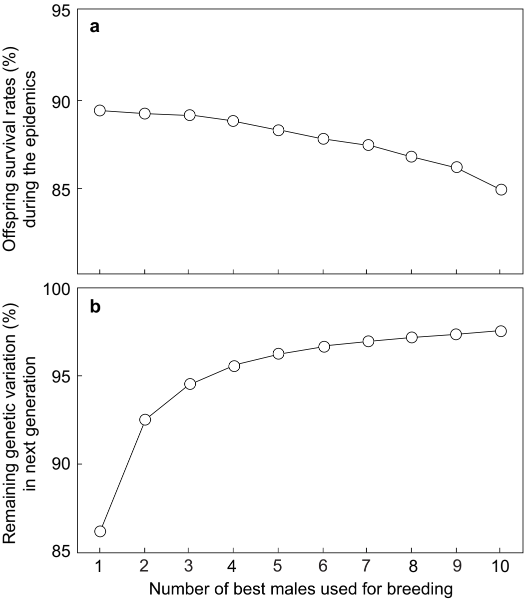

Fig. 3. The calculated egg survival rates during the epidemics (**a**), and the genetic variation (**b**) that would remain in the next generation if only the best male with respect to late egg mortality were used to fertilize all eggs (number of best males used = 1), only the two best males were used and given equal reproductive success (number of best males used = 2), and so on. When all ten males are used, the values correspond to the ones given in Fig. 2 for equalized male and female success.

had the smallest breeding tubercles of all males (0 and 29 μm, i.e. below one standard deviation below the mean of all males) (Fig. 3). Likewise, the worst male had the highest fluctuating asymmetry measured (more than one standard deviation above the mean of all males). These observations suggest that extreme fluctuating asymmetries and breeding tubercles could potentially be used to avoid breeders with low heritable quality.

The fully balanced mating design and the recording of the performance of each family allowed us to estimate the full potential of optimal mate selection with regard to the susceptibility to the epidemics. In Wedekind *et al.* (2001) we had calculated this highest potential egg survival under optimal mate selection (i.e. if we could perfectly predict which male should be mated with which female in order to maximize egg survival). Here, we plotted this theoretical optimum again (Fig. 2c) and calculated the respective variance in reproductive success and the loss of heterozygosity (Fig. 2a and b). In this hypothetical mating scenario, the skew in reproductive success among the males would be optimally linked to egg survival — all else being equal. However, improving offspring survival would again increase inbreeding and the loss of genetic variation (Fig. 2).

Discussion

We found that the males in our study differed greatly in the amount of milt that could be stripped at the hatchery. We did not measure sperm density and sperm quality. However, assuming that the amount of milt is positively linked to the amount of fertile sperm, any breed-

Table 4. Multiple regression of potential *female* quality indicators on early egg mortality (global *F* = 0.06, df = 3, *p* = 0.98), and on late egg mortality (global *F* = 1.50, *p* = 0.31).

Potential quality indicator	Direction of the effect		*F*	*p*
	Expected	Observed		
Early mortality				
Condition factor	–	–	0.12	0.74
Breeding ornamentation	–	+	0.02	0.89
Fluctuating asymmetry	+	–	0.01	0.92
Late mortality				
Condition factor	–	+	2.3	0.18
Breeding ornamentation	–	+	1.6	0.25
Fluctuating asymmetry	+	+	2.0	0.21

ing technique that does not attempt to equalize the reproductive success of the males in the hatchery increases the inbreeding coefficient and thereby the loss of genetic variation in the next generation.

If sperm density and sperm quality varied among the males, mixing equal amounts of milt would probably not result in equalized fertilization success (e.g. due to sperm competition). In other systems, sperm competition has been found to contribute significantly to variance in reproductive success (e.g. Boudry *et al.* (2002) in Pacific oyster, *Crassostrea gigas*). This potential problem could be circumvented in the hatchery by mixing eggs and fertilizing equal batches of eggs separately by the milt of one male each. In this case, milt volume would not have to be equalized.

We did not find a significant correlation between stripped milt volume and offspring mortality. Therefore, if egg survival could not be predicted by any male characteristics, our data suggest that hatchery managers should avoid using all the collected milt equally but instead equalize male reproductive success in the hatchery. This would minimize the loss of genetic variation while keeping the number of offspring unchanged.

Equalizing the females' success in the hatchery would of course reduce the total amount of eggs that could be reared, as some of the eggs would have to be discarded (in our example, the number of eggs per female would have to be reduced to about 4000 each, i.e. about 40% of the total amount of eggs would have to be discarded). The number of eggs that could be stripped per female was not correlated with egg survival. If the situation is such that the number of fertilized eggs in the hatchery does not correspond to the later recruitment rates at high numbers of released fry (as indicated in Fig. 1), equalizing female reproductive success should be preferred over using all eggs as it leads to a reduced inbreeding and hence a reduced loss of genetic variation in the next generation. In other words: under some situations, reducing the number of eggs raised in the hatchery increases N_e in the population.

The total mortality observed here was low as compared with the mortalities observed in other studies on coregonids (Dąbrowski *et al.* 1987, Ventling-Schwank & Müller 1991, Rojas-Beltran & Gillet 1995), despite the epidemics that happened in the present study. Of course, egg survival under our experimental conditions in the laboratory can only give a rough approximation of egg survival in the hatchery or in the wild. This could potentially explain why we did not find a correlation between egg size and egg survival.

We used three types of mate quality indicators: condition factor, size of the breeding tubercles as a measure of the breeding ornamentation, and degree of asymmetry at the pelvic fins. If these three measurements are indeed quality indicators, they seem to reveal different aspects of quality as they did not correlate with one another. Nevertheless, in the males these three potential indicators were all useful predictors of egg survival during an epidemic.

Sexual selection theory predicts that a potential mate's phenotype, and especially its sexual ornamentation, is used to select for heritable viability in the wild (Grahn *et al.* 1998, Westneat & Birkhead 1998, Møller & Alatalo 1999, Jennions & Petrie 2000). The original Hamilton and Zuk hypothesis (Hamilton & Zuk 1982) even predicts a correlation between the males' viability indicators and their offspring's resistance against infectious diseases. Our results suggest such a connection. It seems that the viability measures we took could indeed be used by the hatchery manager to promote egg survival in supportive breeding. An important question is then: how can heritable viability be weighted against the loss of genetic variation? This is a difficult question that can probably not be answered at the moment (Wedekind 2002a, *see* also Fig. 3). However, simply ignoring the issue means assuming that the preservation of genetic variation has priority over promoting heritable viability. This may or may not be the optimal strategy with respect to the long-term viability of a given population.

Up to now we assumed that eggs are either susceptible or resistant to present pathogens, and that pathogen pressure does not interact with the total number (and density) of susceptible eggs. However, this assumption may be overly simplistic. Serial infection experiments suggest that pathogens normally adapt to host genotypes and thereby increase their virulence (Ebert 1998).

Moreover, a typical result of infection experiments is that the establishment of an infection depends on parasite density. Therefore, being surrounded by susceptible eggs is likely to increase parasite pressure on a given egg. If so, a breeding regime that leads to relatively more resistant offspring will not only reduce total mortality because of the increased mean host resistance, but it will also reduce overall parasite pressure on the average egg and thereby further reduce total offspring mortality. As a consequence, giving more resistant parents a higher reproductive success would lead to relatively low N_e/N_c ratio at the time of fertilization as compared with that when equalizing reproductive success among all parents. However, the expected reduced offspring mortality is likely to compensate at least partly for this initial loss of genetic variation.

In conclusion: If the issue of heritable viability were ignored, the individual reproductive success among the males should be equalized at fertilization. Under certain circumstances, equalizing also female reproductive success may result in a maximum N_e (i.e. a minimal loss of genetic variation), although this means that some excess eggs would have to be discarded. In our study, several potential quality indicators varied so much that a hatchery manager would easily be able to identify the extremes by visual and tactile inspection of the fish. We found that in the males, these potential quality indicators were indeed useful in predicting egg survival. Hence, the hatchery manager could potentially increase mean egg survival by taking information about these quality indicators into account. However, it is currently difficult to predict the optimal compromise between promoting heritable viability versus promoting genetic variation. At least: any extensive loss of genetic variation, as, for example, in some scenarios indicated in Fig. 3, should undoubtedly be avoided.

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