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# Using factorial mating designs to increase the effective number of breeders in fish hatcheries

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#### Abstract

We used Monte Carlo simulations to evaluate the potential of full- and partial-factorial mating designs to increase the effective number of breeders in fish hatchery operations, using two probability distributions (normal and uniform) to generate individual fitness values, two methods (multiplicative and additive) of combining fitness values in individual matings, four full-factorial designs ( $10 \times 10$ ,  $20 \times 20$ ,  $40 \times 40$ ,  $120 \times 120$ ), and three partial-factorial designs ( $2 \times 2$ ,  $5 \times 5$ ,  $10 \times 10$ ).  $N_b$  under full-factorial mating was nearly linearly related to, and quite predictable from  $N_b$  under single-pair mating. The higher the variance of family size under single-pair mating, the greater the  $N_b$  benefit of full-factorial mating; and the larger the population, the greater the full-factorial benefit. Under assumptions of additive combination of fitness values, full-factorial mating resulted in an average  $N_b$  increase of 33%. Partial-factorial designs as small as  $2 \times 2$  achieved on average 45% of the  $N_b$  advantage attainable under full-factorial mating. The proportionate incremental  $N_b$  benefit from partial-factorial designs diminishes rapidly as the size of the design increases, but designs as small as  $10 \times 10$  may attain such a large proportion of the full-factorial benefit as to render larger designs unnecessary. © 2007 Elsevier B.V. All rights reserved.

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### 1. Introduction

Maximizing effective population size is a worthwhile objective in virtually all hatchery operations. This is especially true of conservation operations, where the hatchery may play an important role in the maintenance of genetic diversity in the population being cultured, but should also be a consideration in purely aquacultural efforts because of its effect on inbreeding depression, selection intensity, variation in response, and long-term response (Toro and López-Fanjul, 1998). Usually expressed on a per-generation basis, effective size is an average (Waples 2002a, 2004) of the effective number of breeders ( $N_b$ ) in individual spawning seasons.  $N_b$  is determined by the number of breeders of the two sexes and by the variance of family size.

Mating design can have a large effect on the variance of family size. Mass mating involving sperm pooling from a number of individuals, for example, has been shown to increase the variance of family size and thus reduce  $N_b$  considerably over what would be achievable with single-pair mating in pink salmon (*Oncorhynchus gorbuscha*) (Gharrett and Shirley, 1985), Chinook salmon (O. tshawytscha) (Withler, 1988; Withler and Beacham, 1994), Alpine whitefish (*Coregonus zugensis*)

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(Wedekind et al., 2007), and American shad (*Alosa sapidissima*) (Brown et al., 2000). Wedekind et al. (2007) estimated that variability in sperm density and milt volume in mass mating could reduce male  $N_b$  by 40–50%. Although this variability in male potency has been noted in a hatchery environment only in these few species, sperm competition has been noted in numerous fish species, so it is likely that sperm competition, coupled with intrinsic differences in sperm motility and concentration, could cause sperm pooling to reduce  $N_b$  in hatchery operations in many species.

An alternative to gamete pooling is single-pair mating, and this technique is now widely used in some hatchery operations, but single-pair mating has the disadvantage of completely linking the reproductive potential of each fish with its mate. If a male is sterile, not only is there no reproductive contribution from him, there is also none from his mate. Conversely, if a female is mated to a fertile male but all her eggs are immature, neither she nor the male will contribute (Fiumera et al., 2004). The obvious solution is a technique whereby gametes are not pooled, but the risk of little or no contribution is spread over multiple mates. One strategy used to safeguard against the risk of sterile males is the use of overlapping pairwise spawning, where multiple males are mated with a single female (Withler and Beacham, 1994; Campton, 2004). A more general solution is factorial mating, which typically involves dividing the milt from each male and eggs from each female into aliquots so that each female is mated with more than one male and vice versa. In some applications the same effect can be achieved with egg pooling, which is less logistically difficult (Campton, 2004; Dupont-Nivet et al., 2006).

Because of its intuitive appeal in distributing risk, factorial mating is recommended in a number of hatchery manuals, at least in salmonids, but has received relatively little attention in the primary literature. Campton (2004) reviewed different mating types used in salmonid hatcheries and made recommendations for implementing methods such as factorial mating on a large scale, citing in part early data from the present study suggesting that  $N_{\rm b}$  was increased under factorial mating and that approximately 50% of the benefit of a full-factorial design can be achieved with a  $2 \times 2$  partial-factorial design. Fiumera et al. (2004) did both a modeling and application of the method to a conservation operation for redhorse (Moxostoma robustum), an endangered North American cyprinid, and found that factorial mating can increase effective size up to 19%, also noting that a substantial portion of the full-factorial benefit can be achieved with 2×2 matings. Engström et al. (1996) and Dupont-Nivet et al. (2006) approached the subject from

an animal breeding perspective, using models of quantitative genetic variation to compare selection response under single-pair mating and a variety of factorzial mating schemes. They noted that selection response was improved and inbreeding was decreased over multiple generations under factorial mating, and also noted that  $2 \times 2$  partial-factorial matings offered a considerable benefit over single-pair matings.

Although the existing research on factorial mating has already pointed out many of the key results we will present, we felt the subject could benefit from a broader treatment. In this paper we extend the results of earlier studies of the potential of factorial mating to increase the effective number of breeders over what could be achieved using single-pair mating by modeling individual fitness in two ways, using two methods to combine individual fitnesses, and modeling over several sizes of full- and partial-factorial mating designs. Our goals were to explore the sensitivity of results to the simulation elements we varied, and to make broadly applicable generalizations about the benefits of full-factorial over single-pair mating and the benefits of partial-factorial relative to full-factorial designs.

#### 2. Methods

#### 2.1. Simulations

We modeled mating populations in which *N* males were mated to *N* females in single-pair (SP), full-factorial (FF), and partial-factorial (PF) designs. *N* was set at 10, 20, 40, and 120. *N* limited the number of PF designs that we could evaluate because *N* had to be a multiple of the PF array sizes to allow for a whole number of PF arrays of the same size (Fig. 1). Thus, if N=10,  $2 \times 2$  and  $5 \times 5$  PF designs could be applied; if N=20,  $2 \times 2$ ,  $5 \times 5$ , and  $10 \times 10$  PF designs could be applied; etc. PF designs for the full set of simulations were  $2 \times 2$ ,  $5 \times 5$ , and  $10 \times 10$ . Population sizes were both held constant, so 2N progeny were produced. Mean family size for both sexes was thus two.

The key elements of the modeling were mathematically generating variable and biologically plausible fitness values (FVs) and then combining male and female FVs in a biologically plausible way to generate FVs for the individual matings. We used two methods for each, generating FVs from normal or uniform distributions, and then combining male and female values additively or multiplicatively. The actual values used to set variability levels turned out to be unimportant, so long as a sufficient range of variability was achieved, but our actual procedure was as follows. For normal deviates, levels of FV variation were set by using a mean of 500 and applying a variety of coefficients of variation from 1 to 50. Uniform deviates were sampled from the range [1000(-x), 1000(1-x)], where *x* was set at a number of values between 0 and 1. Both normal and uniform distributions resulted in a proportion of negative values,

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