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A Bayesian approach for the genetic tracking of cultured and released individuals

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Abstract

In all supplemental stocking programs, regardless of scale, at least some of the released animals should be tracked (recaptured and identified) to evaluate and quantify the effect of the release on wild stocks. Often, marking these animals extrinsically can be impractical. Here, a parentage-based (familyprinting), Bayesian approach is presented for genetically tracking individuals produced in captivity and released among wild conspecifics. Any class of autosomal, codominant, molecular markers may be used, provided that loci are independent and population genotype frequencies conform to Mendelian expectations for diploid systems. Incorporating reference allele-frequency data from the recipient stock and genotype data from the captive parents, parentage of tested individuals can be established via likelihood ratios that compare the probability of the genetic evidence for coparentage to the probability for coincidence for individuals whose genotypes are compatible with parental pairs. Given a sufficient number of variable loci, products of these likelihood ratios and appropriate prior probabilities yield sufficiently large posterior probabilities of coparentage, i.e., very low expectations for false-positive assignment. Thus, post-release differences in growth, survivorship, or performance traits may be evaluated among groups, among families, or among genotypes and various stocking practices (e.g., size-at-release, release location) can be studied in vivo. The principal benefit of the approach occurs when family sizes of hatchery breeding pairs are considerably larger than those of wild pairs in the stocked population, as expected during successful enhancement. An application of the method to a large-scale stocking program is described, including results of blind performance testing and mutation rate analyses to investigate program error rates.

Keywords: Stock enhancement; Genetic tag; Familyprinting; Red drum; *Sciaenops ocellatus*

1. Introduction

Supplemental stocking has been practiced worldwide at various levels for centuries, but evaluation of post-release survival of stocked fish and their contribution to the fishery is, for the most part, an emergent component of such activities (Leber and Lee, 1997). The need to track released fish with minimal influence on their behavior, health, or survival has led to the development of a variety of extrinsic tags (Guy et al., 1996). Among these are coded wire tags (CWT), passive integrated transponders (PIT tags), body-cavity tags, anchor-type tags, and visible implants. Each tag type has advantages and disadvantages in given applications. For example, PIT tags can be repeatedly 'sampled' without harm to the fish but are expensive; CWTs are comparatively inexpensive but must be extracted from fish to be read. All of the above-listed tags share at least two common disadvantages—there is a lower limit to the size of fish into which they may be safely inserted and a practical upper limit to the number of fish that can be tagged. Because it may be more cost-effective to release large numbers of small fish than small numbers of large fish (e.g., Kent et al., 1995; Wilson et al., 1998), stocking programs may benefit from a method of tracking that is not constrained by the number of fish to be released or their size at release.

Molecular genetic markers have been used extensively to identify and monitor hatchery fish in supplemented stocks (e.g., Murphy et al., 1983; Taggart and Ferguson, 1986;

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Gharett and Seeb, 1990; King et al., 1993; Crozier and Moffett, 1995; Hansen et al., 1995; Tessier et al., 1997; Wilson et al., 1997; Norris et al., 1999; Perez-Enriquez and Nobuhiko, 1999). Mixed-stock and population-assignment analyses (Millar, 1987; Pella and Masuda, 2001) have been used to estimate the relative contributions of hatchery and wild fishes in admixtures (e.g., Hansen et al., 1995; Kamonrat, 1996) and to assign individuals to hatchery or wild stocks (e.g., Hansen et al., 2001; Koskinen et al., 2002). However, because these analyses require sufficiently high levels of genetic heterogeneity between hatchery and wild stocks for precision, they are not readily applicable to all stocking programs, especially those in which broodfish are randomly sampled from the wild each generation.

An alternative approach – familyprinting – has been suggested (Letcher and King, 1999). Familyprinting has been defined as identifying (assigning) the parentage of tested individuals. Like most mixed-stock analyses, familyprinting involves the use of multilocus genotype data. Computer simulations have indicated that familyprinting could potentially be used to determine the parental pairs of progeny sampled from a genetically homogeneous (unstructured) population (Letcher and King, 1999; Bernatchez and Duchesne, 2000; Eldridge et al., 2002). Unfortunately, no theoretic framework has been proposed for evaluating levels of confidence in parental-pair assignments on a case-by-case basis. Investigators have instead relied on post hoc simulations to estimate the group-wise power of their loci to correctly include or exclude parentage. As reviewed by Jones and Ardren (2003), such simulations do not take advantage of all available information and may be biologically unrealistic because they rely on assumptions of random mating (e.g., within and among hatchery and wild breeders) and binomial variance in family size. They also require and are sensitive to an estimate of the total (hatchery and wild) number of breeding pairs per generation interval, N_{HW}, in the system, which, in the case of marine stock enhancement, is expected to be quite large ($>10^4$). When system-wide random mating is assumed, statistical power for hatchery parental assignments declines rapidly as N_{HW} increases.

In most cases, however, hatchery breeders are segregated from wild breeders. When the stocking program is relatively effective, the reproductive successes of hatchery breeding pairs are considerably greater on average than those of wild breeding pairs in the system. Consequently, parentage probabilities for offspring of hatchery breeding pairs in hatchery/wild admixtures are expected to be higher than standard simulations would predict. Here, I present a Bayesian framework for a parentage-based method of tracking individuals produced in captivity and released into wild populations wherein probabilities of correctly assigning parentage can be computed directly for each tested individual. When the probabilities are appropriately conditioned, the need for post hoc power estimation is circumvented and relevant issues involving family structure are addressed. General application of the method to the post-release monitoring of captive-bred fish is discussed and illustrated via a case study of an ongoing stocking program for red drum (*Sciaenops ocellatus*).

1.1. Marker-based parentage testing

Bayesian methods may be used to examine the probability that a hypothesis ($H1$) is true given the observed data, relative to one or more competing hypotheses (e.g., $H2$). A *prior probability* – the probability that a hypothesis is true prior to consideration of the observed data – may be specified. The prior probability is based on prior or conditioning information (I). The term *likelihood* is used to describe the conditional probability of observing the new data (D) given a particular hypothesis. The likelihood ratio (L) is the ratio of two probabilities of obtaining D under competing hypotheses. The term *posterior probability* refers to the probability that $H1$ is true given D and I. Bayes' well-known theorem (Bayes, 1763) states that

$$\frac{\Pr(H1|D, I)}{\Pr(H2|D, I)} = \frac{\Pr(D|H1, I)}{\Pr(D|H2, I)} \frac{\Pr(H1|I)}{\Pr(H2|I)}, \quad (1)$$

or

$$\text{posterior odds} = \text{likelihood ratio} \times \text{prior odds},$$

where the odds for two events is the ratio of their probabilities. When alternative hypotheses are evaluated, $\Pr(H2|D, I) = 1 - \Pr(H1|D, I)$ and $\Pr(H2|I) = 1 - \Pr(H1|I)$; thus, posterior odds may be converted to posterior probabilities by rewriting Eq. (1) to give

$$\Pr(H1|D, I) = \frac{\Pr(H1|I) \times L}{[1 - \Pr(H1|I)] + \Pr(H1|I) \times L}. \quad (2)$$

Because likelihood ratios are proportional to probabilities, the multiplicative law may be applied over multiple, independent sets of data (e.g., multiple, unlinked loci) to obtain a likelihood ratio on the combined data (Edwards, 1992).

The statistical approach for genetic tracking is based on computation of the joint probability of maternity and paternity, which, in Bayesian terms, may be described as the *posterior probability of coparentage*, $\Pr(\text{CP}|D, I)$. In other words, we seek to determine if a tested individual is the offspring of a specific parental pair (mother and father), whose multilocus genotypes are known. For brevity, the terms D and I will be hereafter omitted from posterior probabilities. The posterior probability Pr(CP) may be referred to generically as an *assignment probability* in that it may be used to assign a tested individual to a parental pair. To do so, multilocus genotypes for the tested individual, the putative mother and the putative father are examined. For each locus, the conditional likelihood ratio for coparentage (L_{CP}) may be taken as the quotient X_{CP}/Y_{CP}, where X_{CP} and Y_{CP} specify the following probabilities:

- $X_{CP} = \Pr\{$observing the tested individual's genotype when the putative mother and father are the actual parents$\}$.