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Levels of inbreeding in group mating captive broodstock populations of Common sole, (*Solea solea*), inferred from parental relatedness and contribution

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ABSTRACT

In this paper, we estimate levels of inbreeding with parental relatedness and contribution inferred from microsatellites in groups of Common sole that reproduce by natural mating. We present results on spawning patterns during one entire reproductive season of wild Common sole, *Solea solea,* kept in two broodstock groups (28 animals in broodstock A; 20 animals in broodstock B) under semi-natural conditions. Batches of eggs were collected daily and incubated separately. First, we performed a parentage analysis on parents and samples of 24 newly hatched larvae from all batches, using 10 polymorphic microsatellite markers. As expected, contribution of parents to offspring was highly skewed. In both broodstocks, five or less parental pairs produced more than half of the total progeny. Natural spawning and unequal contributions of parents to offspring resulted in significant deviations from Hardy–Weinberg equilibria. Furthermore, few alleles were lost and levels of heterozygosity in offspring population increased. Next, we calculated relatedness between parents that mated successfully based on estimates of molecular similarity. Mean coefficients of coancestry in offspring were determined using parental relatedness and contributions. Levels of coancestry in progeny were substantially high. These results show that due to different parental contributions, natural mating in groups can result in significant inbreeding in future generations despite of limited loss of alleles and high levels of heterozygosity in first generation progeny. This shows that using loss of alleles and levels of heterozygosity alone can be misleading for estimation of genetic diversity.

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1. Introduction

Most livestock breeding programmes use controlled reproduction methods like artificial insemination, or natural mating of couples to control family structures and pedigree. This is of major importance when executing breeding programmes with restriction on level of inbreeding (Bijma et al., 2000; Dupont-Nivet et al., 2006; Henderson, 1984).

In some fish species controlled reproduction is a relatively easy matter. For example, in salmonids (Billard, 1992), carps, *Cyprinus* spp. (Billard, 1995), turbot, *Scophthalmus maximus* (Chereguini et al., 1999) and African catfish, *Clarias gariepinus* (Goos and Richter, 1995) artificial fertilization is used. A problem occurs when reproduction is dependent on natural mating of animals kept in groups. Natural mating in groups often results in production of massive and variable family sizes of unknown pedigree (Gjerde et al., 1996; Komen et al., 2006). Furthermore, only a restricted number of animals (especially in males) contribute to majority of the descendants. Such skewed contributions have been shown in Nile tilapia, *Oreochromis niloticus* in hapas (Fessehaye et al., 2006), Atlantic cod, *Gadus morhua* (Bekkevold, 2006; Bekkevold et al., 2002; Rowe, 2007) and in Gilthead seabream, *Sparus aurata* (Brown et al., 2005).

In sole it is still difficult to induce spawning by artificial means. Therefore, natural mating in groups is used (Dinis, 1999; Howell et al., 2006; Imsland et al., 2003). Natural mating behaviour of Common sole was described by Baynes et al. (1994).

Consequences of natural mating in fish species are usually analyzed with classical population genetic approaches (e.g., Exadactylos, 1999; Perez-Enriquez et al., 1999; Porta et al., 2006a). In these cases, inbreeding and genetic variability are analyzed using loss of alleles and levels of heterozygosity such as F_{IS}. However, when performing directional selection, these methods can not be used to predict consequences of natural mating for populations. Additive genetic relationships on the other hand, are widely used to estimate genetic parameters and breeding values of individuals. Further, they can be used to optimize selection designs in terms of minimizing inbreeding, e.g. through optimal contribution (Sanchez et al., 2003). When pedigree information is absent, relatedness can be inferred from molecular markers (reviewed in Oliehoek et al., 2006). In this paper we present a method to analyze levels of inbreeding in species that reproduce by natural mating in groups, using estimates of parental relatedness together with contribution. Our results show that

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natural mating in groups leads towards an increased mean coefficient of (molecular) co-ancestry in offspring of sole. This is in contrast with traditional population genetic analysis where heterozygosity in progeny increases.

2. Materials and methods

2.1. Broodstock

Two Common sole broodstock populations A (n=28) and B (n=20) were collected from the Dutch North-Western coastal area during 2003 through 2005. From collection up to start of the experiment both broodstocks were conditioned indoor in separate tanks. Mean body lengths and weights are shown in Table 1 Broodstocks were fed a diet of moist pellets and polychaetes to 0.5% of their bodyweight every second day. During the spawning period the diet was given ad libitum.

2.2. Broodstock management

Each broodstock tank had a diameter of approximately 3 m and a height of 1.40 m. Salinity was 34 ppt. Each tank had a sand bottom of approximately 5 cm. Both tanks were connected to one recirculation system (total volume 70 m^3). Artificial temperature and light regimes were controlled per tank separately and simulated those of natural circumstances (52°N and 2.5°E) with a six months difference between broodstocks. In broodstock A, spawning commenced on June the 28th of 2006 and lasted until October the 12th. Spawning of broodstock B lasted from January the 2nd of 2007 until May the 5th. Every three weeks spawning was suspended artificially for one week by lowering water temperature.

2.3. Egg collection

Pelagic eggs were continuously collected at the out flow of the spawning tank. Every morning at approximately 09.00 h, all eggs were harvested from the egg collector and kept as one separate batch during subsequent incubation and larval rearing. Each batch was weighed and egg quality was evaluated as “low”, “moderate” or “good”. Batches were incubated subsequently in a conical incubation tank of approximately 80 l. Each incubation tank was connected to a recirculating system with UV-treatment. Incubation temperatures were 10 °C and hatching took place after three days incubation.

Every day from day 0 until hatching, sinking eggs were drawn off and weighed. From these data the approximate number of hatched eggs per batch was calculated:

$$\mathrm{He}_i = \left(\mathrm{Wt}_i - \sum_{j=1}^{n} (Ws_{ij})\right) \cdot \rho e \tag{1}$$

where He_i is number of hatched eggs of batch i, Wt_i is weight (g) of eggs of batch i at time of collection and Ws_{ij} is weight (g) of sinking eggs of batch i at day j. Pe is number of eggs per g which was determined at start of the spawning season by counting numbers of eggs in approximately 1 g of eggs.

Due to restricted capacity in the incubation system several small batches had to be incubated in small floating 1-l tubes within the same incubation system. From small batches sinking eggs could not be measured as these quantities were generally too small for accurate weighing. Instead hatching percentages were estimated from average hatching percentages in large batches with similar evaluated quality (i.e. low, moderate and good) according to:

$$\mathrm{He}_{ik} = \mathrm{Wt}_{ik} \cdot \mathrm{Hp}_k \cdot \rho e \tag{2}$$

where He_{ij} is number of hatched eggs of batch i with quality k, Wt is total weight (g) of eggs in the small batch at day of collection i and Hp is predicted hatching rate at quality k in large batches. Pe is number of eggs per g.

Table 1
Number of parents, mean body weight (BW) (±SD), body length (BL) (±SD), mean hatching rate (Hr) and estimated number of produced larvae (L) per broodstock (BS)

BS		n	BW (g)	BL (mm)	Hr (%)	L (106)
A	Males	14	504.9 (102.5)	36.2 (2.7)	36	1.2
	Females	14	836.5 (218.6)	42.6 (2.9)		
B	Males	10	476.8 (128.2)	36.5 (2.7)	30	2.5
	Females	10	977 (143.1)	45.7 (3.1)		

2.4. DNA sampling and analysis

Before the experiment, a blood sample of each parent was taken for DNA analysis. Samples were stored in EDTA 0.27 M in physiological salt (0.8% NaCl) solution at −80 °C. For DNA isolation of parental blood, Puregene DNA purification kit for non-mammalian whole blood samples (Gentra Systems) was used. Sampling of larvae for DNA analysis was performed before first feeding at 3–4 days post hatch. From each batch, 24 larvae were sampled at random from the incubator and processed individually for DNA isolation using nucleospin tissue columns (96 procedure, Machery–Nagel). To test if DNA was extracted successfully, DNA concentrations were measured from several samples in all plates using a spectrophotometer (Nanodrop technologies ND-1000). For all samples DNA concentration was diluted to 5–10 ng/µl for further analysis.

The following 10 microsatellite markers were used for DNA analysis: AF173855, AF173854, AF173852, AF173849 (Iyengar et al., 2000), AY950593, AY950592, AY950591, AY950589, AY950588, AY950587 (Garoia et al., 2006).

PCR amplification involved 5 min of denaturation at 95 °C followed by 36 cycles of consecutively 30 s denaturation at 95 °C, 45 s annealing at 55 °C and 90 s elongation at 72 °C. After 36 cycles, a final elongation step of 10 min at 72 °C was applied. After PCR amplification, marker samples were pooled per individual and analyzed on an ABI 3730 automatic sequencer. Fragment sizes were set relatively to Genescan LIZ 500 size standard (Applied Biosystems). Output data was analyzed using Genemapper software (Applied Biosystems) in order to determine allele profiles at each locus. Parental allocation was performed with PAPA 2.0 software (Duchesne et al., 2002). Papa 2.0 is a software package which performs parental allocation by calculating breeding likelihood of a parental pair of (multilocus) genotypes producing a given offspring genotype. It allows a certain degree of genotyping error or mutation. The breeding couple with highest likelihood is defined as the most likely parental pair. Results were manually checked for correct allocation according to Mendelian inheritance afterwards.

2.5. Contribution of parents

Using genotyped larvae, contribution of parents and parental pairs to total offspring was calculated relatively to the total number of larvae produced. This was done for both broodstocks separately.

2.6. Population genetics

Expected and observed heterozygosities, resulting fixation rates (F_{IS}) after Weir and Cockerham (1984), Hardy–Weinberg exact tests and probability tests for differentiation of allelic distribution were calculated with Genepop web application (Raymond and Rousset, 1995). Calculations were performed for parental and offspring populations separately. Further, broodstock A and B were analyzed separately as well as pooled. Expected heterozygosities were calculated using observed allele frequencies from the same population.

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