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Effects of inbreeding on growth and WSSV resistance of the juvenile Chinese shrimp, *Fenneropenaeus chinensis*

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Abstract: To date, few studies had investigated the effects of inbreeding on growth and disease resistance, although inbreeding depression of such traits could play an important role in the evolution and ecology in Chinese shrimp, *Fenneropenaeus chinensis*. Effects of inbreeding on body weight and survival time post infection WSSV of juvenile shrimp were quantified in this study. All families were reared under the similar environment conditions, and the differences of growth time between two groups were not significant. The mean body weight and mean survival time of the wild shrimp group were (1.58 ± 0.01) g and (100.43 ± 0.68) h, and those of the shrimp group with inbreeding coefficient 25% were (1.43 ± 0.04) g and (85.84 ± 1.70) h, respectively. The differences of body weight and survival time post infection WSSV between two groups were all extremely significant ($P < 0.01$). The difference of phenotypic correlation was not significant ($P > 0.05$) between body weight and WSSV resistance of the wild shrimp group, which is 0.16 ± 0.00, and the inbred shrimp group, which is 0.20 ± 0.00. In this study the estimated inbreeding depression coefficient was −3.80% ± 0.17% for body weight and −5.81% ± 0.11% for survival time post infection WSSV per 10% increase in inbreeding coefficient. Results were consistent with the viewpoint that inbreeding could reduce growth and disease resistance. Those highlight the need to maximize the genetic diversity in base population, and to control the rate of inbreeding in selective breeding programs and wild resource protection.

Key words: *Fenneropenaeus chinensis*; inbreeding; inbreeding depression; body weight; survival time; WSSV resistance

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1 Introduction

As aquaculture industry aims to meet the growing world demand, there is a need to dramatically increase production. With the increasing prevalence of disease and limited supplies of wild broodstock, domestication and selective breeding approaches are being increasingly used to improve production efficiency. Through selection of performance traits such as growth, survival and disease resistance, selective breeding programs can produce reliable supplies of healthy seedstock with improved production performance.

There is an increasing trend towards domestication and selective breeding programs for

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shrimp aquaculture with the development of breeding technologies. However, shrimp farming is still in the early stages of domestication and selective breeding compared to most livestock and fish industries[1]. In most cases, these breeding programs have been initiated using a narrow genetic range of base populations, and are maintained through mass selection of a single trait[2]. Breeding programs for livestock and fish industries have shown that selection programs with uncontrolled mating and small breeding populations can lead to inbreeding, the decrease in genetic variation of the population and the subsequent depression of performance traits [3-4].

All finite populations experience some degree of inbreeding[5]. Inbreeding is defined as the probability of two alleles in an individual being identical by descent, and is the result of mating related individuals. The degree of relationship between mating pairs is measured as the coefficient of inbreeding. The inbreeding coefficient (F) is the probability that two alleles at any locus are identical and descended from the same ancestor. Inbreeding limits the potential response to selection of subsequent generations and increases the potential for inbreeding depression[6-7]. Inbreeding depression refers to the effect of inbreeding normally measured as the reduction in the expected performance of the affected trait and is measured as the average performance difference between the inbred population and the base or less inbred population. Fitness-related traits that severely exhibit inbreeding depression are generally affected by multi-loci with non-additive gene effects, for example, productive capacity (e. g. fecundity, egg size, hatchability, growth, diseases resistance) and physiological efficiency (e. g. fry deformities, growth rate, food conversion ratio, survival) [8-10]. And inbreeding may also influence secondary sexual traits, such as color patterns[11], and reduce the salinity tolerance[12-13] as an indication of less tolerance of inbred individuals to environmental changes.

Inbreeding can be controlled partly by enlarging effective number of the base population because recessive deleterious mutations occur at low frequency, meaning that they are seldom expressed. The partial dominance hypothesis is empirically perhaps the best supported model of inbreeding depression[14-15], and suggests that the increase in homozygosity of loci during inbreeding exposes the mutation load of deleterious recessives. However, more and more researchers begin to support the over-dominance hypothesis, which suggests that inbreeding reduces the frequency of superior heterozygotes, resulting in observed fitness loss because inbreeding depression can be potentially reinforced by epistatic effects between loci, resulting in a nonlinear decline of phenotypic value with inbreeding coefficient[16-17]. While inbreeding often is mentioned as a major reason for the loss of productivity in finite populations of aquaculture species, less have been done to solve the problems with inbreeding because not all inbred populations experience significant inbreeding depression[3,18]. Additionally, the relationship between inbreeding and inbreeding depression is not always linear[19]. The magnitude of inbreeding depression may vary considerably depending on the species and the trait examined. And with reference to the development of certain breeds of common carp (e. g. Jian carp), it has even been argued that inbreeding is not of major concern in the management of aquaculture species [20]. Therefore, it is necessary to quantify inbreeding effects of the importantly economical traits and to incorporate this information into the design of breeding programs to improve shrimp performance and fitness.

To date, effects of inbreeding on shrimp growth and disease resistance are poorly understood. The aim of selective breeding programs to maximize superior performances can lead to inbreeding. Additionally, the high fecundity of shrimp, together with their short generation

time, the ability to replace a whole population with very few individuals, and the practice of using fewer males than females in mating situations increase the changes of inbreeding [21-22].

This study aims to quantify the effects of inbreeding on body weight and survival time post infection WSSV of Chinese shrimp, *F. chinensis*. A better understanding of the effects of inbreeding on production and fitness will permit the design of improved selective breeding programs for penaeids.

2 Materials and methods

2.1 Production and management of all families

The wild shrimp captured from Qingdao sea area in China, Rushan Bay in China, and the southern seacoast of Korean Peninsula were named as QD, RS and SK populations, respectively. We supposed that the inbreeding coefficients of all wild breeders were zero. 3 inbred families were obtained by brother-sister mating, and the inbreeding coefficient was 25%. All families were constructed by manual insemination, and placed in individual tanks until they reached a body size suitable for tagging (average 0.60 g). 10 shrimp per family were sampled randomly to detect WSSV before tagging, and all families showed negative results. The spawning time and culturing environment of every family were similar.

2.2 Challenge test

Twenty moribund symptomatic animals were taken from a confirmed WSSV infected pond. Cephalothoraxes from twenty animals were tested by nested PCR and confirmatory histology. The remaining parts were used to infect healthy juvenile *F. chinensis*.

A total of 1460 animals, including of 1300 from 40 wild shrimp families and 160 from 3 inbred families produced by brother-sister mating, were involved in the WSSV challenge tests. All juveniles of every family were distributed averagely into three 2.5 m^3 tanks after tagging. Thus approximately 500 shrimps were raised in every tank. The juveniles had been fed nothing for one day before infecting. Then juveniles were orally infected superfluously with WSSV-infected minced muscle tissue for two consecutive days. The seawater was filtered by sand bed at (25.5 ± 0.9) ℃. Shrimp were fed a commercial feed with 25% protein three times a day, except when they were fed infected tissue.

Dead or moribund animals were removed from the tanks every two hours, and water on the body surfaces was dried off, and their family codes, body weight, tank codes and the time of removal were recorded. In order to verify the infection by WSSV, material from moribund animals was preserved for PCR diagnosis. 164 hours were maintained from animals contacting WSSV to experiment termination.

2.3 Analysis

The mean body weight and mean survival time post infection WSSV, together with their standard error, phenotypic correlation and difference compare, were obtained directly from SPSS11.5 procedure.

The inbreeding depression coefficients, IDC, and the standard error, se, for growth and WSSV resistance were evaluated by using a first-order Taylor series approximation [23], as follows:

$$IDC = \frac{(1 - \frac{\overline{W}_{\text{inbred}}}{\overline{W}})}{(F - F_{\text{inbred}})}$$

Where $\overline{W}_{\text{inbred}}$ and $\overline{W}$ represent the mean body weight or mean survival time post infection WSSV of the inbreeding shrimp group and the wild shrimp group, respectively. F_{inbred} and F represent their inbreeding coefficients, respectively.

3 Results

An important feature of the experiment was that all shrimp must be reared in the same environmental conditions. Rearing the wild shrimp group in parallel with the inbred shrimp groups ($F = 25\%$) made it possible to estimate reasonably the inbreeding effects on growth and WSSV resistance. Families produced by the wild shrimp , whose mean body

weight was (1.58 ± 0.01) g (Table 1), grew significantly faster than the inbred families, whose mean body weight was (1.43 ± 0.04) g (Table 2). And the estimated inbreeding depression coefficient was − 3.80% ± 0.17% per 10% increase in F (Table 3).

Tab. 1 Body weight and survival time post infection WSSV of the first generations

family	number	mean body weight ± s.e. (g)	variance coefficient of body weight (%)	mean survival time[a] ± s.e. (h)	variance coefficient of survival time (%)	phenotypic correlation
1	35	1.48 ± 0.06	26.11	107.37 ± 4.51	24.88	0.31 ± 0.07
2	35	1.69 ± 0.07	24.64	114.46 ± 4.09	21.15	0.11 ± 0.49
3	30	1.44 ± 0.07	28.83	98.33 ± 4.22	23.55	0.15 ± 0.41
4	30	1.55 ± 0.06	21.4	96.07 ± 4.48	25.57	0.19 ± 0.30
5	30	1.63 ± 0.05	18.77	94.93 ± 3.78	21.83	0.17 ± 0.35
6	35	1.41 ± 0.04	18.19	105.54 ± 4.10	23.01	0.29 ± 0.09
7	35	1.65 ± 0.07	27.36	109.31 ± 4.51	24.42	0.48** ± 0.00
8	35	2.05 ± 0.08	23.84	108.11 ± 4.65	25.45	0.50** ± 0.00
9	35	2.33 ± 0.08	20.6	101.66 ± 3.89	22.66	0.30 ± 0.07
10	35	1.50 ± 0.07	30.85	95.77 ± 2.13	13.17	0.36* ± 0.03
11	35	1.60 ± 0.05	20.05	104.74 ± 4.85	27.44	0.13 ± 0.43
12	35	1.50 ± 0.06	25.45	99.03 ± 4.54	27.15	0.17 ± 0.32
13	35	1.68 ± 0.06	21.33	101.43 ± 4.63	27.01	0.19 ± 0.25
14	35	1.15 ± 0.03	18.3	108.86 ± 4.73	25.75	0.46** ± 0.00
15	35	1.53 ± 0.08	32.79	100.17 ± 4.07	24.04	0.04 ± 0.80
16	30	2.00 ± 0.06	18.17	120.40 ± 5.23	23.83	0.01 ± 0.96
17	35	1.34 ± 0.04	21.46	104.91 ± 4.14	23.35	0.13 ± 0.45*
18	30	1.59 ± 0.04	15.78	108.40 ± 4.69	23.72	0.03 ± 0.88
19	35	1.69 ± 0.08	28.9	90.51 ± 3.44	22.49	0.32 ± 0.06
20	35	1.87 ± 0.04	14.73	101.77 ± 2.50	14.56	0.46** ± 0.00
21	30	1.68 ± 0.06	20.2	107.53 ± 4.53	23.1	0.10 ± 0.59
22	30	1.36 ± 0.08	33.54	92.93 ± 4.39	25.91	0.10 ± 0.61
23	30	2.65 ± 0.10	22.19	100.87 ± 3.86	20.98	0.02 ± 0.92
24	35	1.30 ± 0.04	19.13	112.69 ± 4.83	25.36	0.09 ± 0.58
25	35	0.96 ± 0.03	22.94	100.40 ± 4.98	29.39	0.20 ± 0.20
26	30	1.12 ± 0.07	50.82	86.11 ± 4.36	21.51	0.16 ± 0.51
27	30	1.19 ± 0.08	40.22	87.17 ± 3.51	21.69	0.01 ± 0.98
28	30	1.40 ± 0.13	50.61	97.44 ± 4.06	20.83	0.22 ± 0.27
29	30	1.44 ± 0.08	31.23	88.71 ± 3.74	22.33	0.02 ± 0.90
30	30	1.52 ± 0.09	32.01	100.30 ± 4.07	21.08	0.03 ± 0.86
31	30	1.41 ± 0.07	28.78	107.93 ± 3.42	17.07	0.08 ± 0.66
32	30	1.40 ± 0.08	29.75	96.40 ± 3.84	19.92	0.45* ± 0.02
33	30	1.57 ± 0.07	23.41	78.26 ± 2.70	16.6	0.13 ± 0.54
34	30	1.86 ± 0.06	18.71	96.20 ± 3.96	22.55	0.30 ± 0.10
35	35	1.34 ± 0.07	31.75	97.03 ± 3.56	21.72	0.49** ± 0.00
36	35	1.46 ± 0.04	17.56	92.23 ± 3.20	20.55	0.15 ± 0.37
37	35	1.58 ± 0.05	22.02	98.91 ± 3.58	21.46	0.64** ± 0.00
38	30	1.69 ± 0.10	37.87	94.80 ± 4.61	24.33	0.26 ± 0.20
39	30	1.32 ± 0.10	46.47	104.21 ± 4.23	21.51	0.11 ± 0.56
40	30	1.98 ± 0.10	31.58	87.64 ± 2.99	18.09	0.44* ± 0.02
total	1300	1.58 ± 0.01	32.90	100.43 ± 0.68	24.17	0.16** ± 0.00

Notes: [a] survival time was the persisting time from animal contacting WSSV to death, and if animal had been live in the end of the experiment, we had named its survival time as 164 h.

* denoted significant phenotypic correlation between body weight and survival time (Tukey's test, $P < 0.05$).

** denoted significant phenotypic correlation between body weight and survival time (Tukey's test, $P < 0.01$)

In terms of WSSV resistance families produced by the wild shrimp, whose mean survival time was (100.43 ± 0.68) h (Table 1), survived longer than the inbred families, whose mean survival time was (85.84 ± 1.70) h (Table 2). The estimated inbreeding depression coefficient was −5.81% ± 0.11% for 10% increase in F. And the differences of body weight and WSSV resistance between two groups were all statistically significant ($P < 0.01$) (Table 3).

Phenotypic correlations between body weight and survival time were different in the wild shrimp group, whose mean correlative coefficients were 0.16 ± 0.00 (Table 1), and the inbred shrimp group, whose mean correlative coefficients were 0.20 ± 0.00 (Table 2). But the difference of correlative coefficients was not significant statistically ($P > 0.05$).

Tab. 2 Body weight and survival time post infection WSSV of inbred families produced by brother-sister mating

family	number	mean body weight ± s.e.	variance coefficient of body weight (%)	mean survival time(h) ± s.e.	variance coefficient of survival time (%)	phenotypic correlation
1	30	1.11 ± 0.06	30.17	79.62 ± 2.89	18.55	0.17 ± 0.16
2	30	1.43 ± 0.09	32.84	101.08 ± 4.58	22.22	0.13 ± 0.27
3	100	1.52 ± 0.05	34.9	83.73 ± 2.02	23.87	0.24* ± 0.02
total	160	1.43 ± 0.04	35.73	85.84 ± 1.70	24.09	0.20** ± 0.00

Tab. 3 Estimates and comparison between the first generation and inbred families

traits	F (%)	inbreeding depression (10% unit increase in F)	t-test in the first generation and inbred families
body weight	25	−3.80% ± 0.17%	3.27 ± 0.00
survival time	25	−5.81% ± 0.11%	6.99 ± 0.00
phenotypic correlation	–	–	0.96 ± 0.37

4 Discussion

Inbreeding is unavoidable in closed populations particularly those undergoing selection. Recently inbreeding in nature population has also received attention with about 75% of the world's marine stocks are fully exploited or overexploited[24]. Generally, inbreeding has a bigger negative effect than the positive effect on the economical traits[25]. Unless managed strategically, inbreeding itself is almost universally harmful and breeders normally seek to avoid levels which produce inbreeding depression[1,5,26]. However, the magnitude of inbreeding depression may vary considerably depending on the species, the level of inbreeding and the trait examined[6]. Most of the published data on inbreeding and inbreeding depression in aquaculture species were recorded on salmonid species[10]. And all researches on shrimp and mollusks had also supported the general viewpoint of Keller and Waller[27] that inbreeding could reduce growth and disease resistance and restrain the selective response. Traits related to the overall fitness of aquaculture species showed inbreeding depression in the range of 3% − 50% per 10% inbreeding[28-30]. In this study levels of inbreeding of $F = 25\%$ had a significantly negative effect on growth and WSSV resistance. Estimated inbreeding depression coefficients were −3.80% ± 0.17% (per 10% increase in F) for growth and −5.81% ± 0.11% for WSSV resistance. Results were consistent with the viewpoints of Sheng and Yao[31] that inbreeding depression had less effect on the high heritability traits than the low heritability traits.

Inbreeding had effects on the performance and potential for maximum selection response in closed populations of *P. stylirostris*[4,32] and *P. japonicus*[33]. However this was the first report to quantily statistically inbreeding and inbreeding depression in *F. chinensis*, which was very important to selective breeding programs and wild resource protection.

Although selection could reduce the effects of low inbreeding depression in the first few generations, Su *et al*[34]. suggested that accumulated levels of inbreeding could ultimately reach critical levels where shrimp performance would be impaired by inbreeding depression. Selective and breeding populations in Tahiti and New Caledonia had showed many signs of inbreeding depression and limited selective response potential for 17 years [4,32]. There was a trend for growth and WSSV resistance to be negatively affected by inbred families produced from brother-sister mating in this study when *F. chinensis* average body weight was 1.43 – 1.58 g.

The conventionally accepted cause of inbreeding depression is that the expression of deleterious recessive or partially recessive alleles in homozygous form causes reduced fitness among the offspring of inbred parents (partial dominance model). Many researches had suggested that inbreeding depression could be reduced or reversed by natural selection and hybrid populations that had a history of inbreeding were expected to be less susceptible to inbreeding depression to some extent. The magnitude of inbreeding depression of *Drosophila melanogaster* in the purged populations was approximately one-third of that observed in the original base population[35]. However, if inbreeding depression was caused by deleterious recessive alleles clustered into a large linkage group (associative overdominance), as had been suggested in experiments on *E. texana* [36], then purging of inbreeding depression would be unlikely and the estimates of inbreeding depression would be considered robust. Indirect evidence for such a linkage group had been suggested because of the general lack of purging in many experiments, which suggests a large linkage group containing several fitness-related loci was a major contributor to inbreeding depression[37]. Deleterious mutating within this linkage group would be difficult to purge, and may tend to accumulate. Deleterious alleles outside this linkage group should be capable of being purged. Inbreeding depression could be detected likely in all inbreeding population due to many deleterious loci contained within the linkage group.

Fast inbreeding through sib-mating resulted, on average, in three times higher inbreeding depression compared to slow inbreeding in large-scale selective breeding programs. Inbreeding depression would be lower if it measured in closed populations with moderate rates of inbreeding than systematically inbred populations. Since our study utilized the inbred families produced by brother-sister mating, perhaps we had an overestimation of inbreeding depression for body weight and WSSV resistance. However, many results suggested that inbreeding depression was still evident in populations with low to moderate levels of inbreeding as the accumulation of inbreeding coefficient for many generations[26,38-39].

Although inbreeding is virtually unavoidable in hatchery populations because of their restricted population size, efforts should be made to restrict inbreeding and its negative consequences on the production efficiency of aquaculture species. More full-sib families are required in selective breeding programs than in ordinary hatcheries, to allow highest possible selection intensity while maintaining a large additive genetic variation and restricting inbreeding depression in the breeding population.

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控制环境养殖下近交对中国对虾早期体重和抗 WSSV 性状的影响

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摘要：过量的捕捞和不合理的人工育种措施，使中国对虾野生和养殖群体的遗传多样性均遭到不同程度的降低。本试验在相似的环境条件下养殖了 40 个野生对虾产生的家系和 3 个兄妹交产生的家系，定量测定了平均体重（1.43 ~ 1.58） g 1 460 尾中国对虾早期体重和感染白斑综合征病毒（WSSV）后存活时间的近交衰退系数。结果显示，野生对虾家系组的平均体重和平均存活时间分别为（1.58 ±0.01） g 和（100.43 ±0.68） h，而兄妹交家系组平均体重和平均存活时间分别是（1.43 ±0.04） g 和（85.84 ±1.70） h，平均体重和平均存活时间在两组间均存在极显著差异（$P < 0.01$）。野生对虾家系组体重和存活时间的表型相关系数为 0.16 ± 0.00，而兄妹交家系组两者间的表型相关系数为 0.20 ±0.00，但是两组间表型相关系数差异不显著（$P > 0.05$）。近交系数每增加 10%，体重和感染 WSSV 后存活时间分别衰退 −3.80% ±0.17% 和 −5.81% ±0.11%，与近交能够降低生长和疾病抗性的观点相一致。实验结果表明，在选择育种和种质资源保护过程中都应该保证基础群体遗传背景最大化，从而有效控制近交。

关键词：中国对虾；近交；近交衰退；体重；存活时间；抗 WSSV 性状

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