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刺参耳状幼体体长遗传力的估计

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摘要:基于全同胞组内相关法估计刺参(*Apostichopus japonicus* Selenka)耳状幼体初中期体长的遗传力。实验中的30个亲参来自人工养殖的成体刺参群体,亲本交配采用巢式不平衡设计,通过人工授精技术,构建了8个半同胞家系和22个全同胞家系。在耳状幼体初期和中期,每个全同胞家系分别测定40~70个后代个体体长。利用SAS软件的GLM过程,计算表型变量的原因方差组分,估算体长遗传力。分析结果显示,雌性遗传方差组分均显著大于雄性遗传方差组分($P<0.05$),雌性遗传方差组分存在显著的母性效应($P<0.05$)。基于父系半同胞组内相关法计算的狭义遗传力是刺参耳状幼体初中期体长狭义遗传力的无偏估计值,估计值分别为0.74和0.75。结果表明,基于刺参耳状幼体体长的加性遗传方差较大,选择育种对于刺参幼体早期生长的改良具有较大的潜力。[中国水产科学,2006,13(3):378-383]

关键词:刺参;遗传力;全同胞

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刺参(*Apostichopus japonicus* Selenka)是海味珍品之一,含有丰富的蛋白质和黏多糖,营养和药用价值高。刺参自然资源主要分布在北太平洋沿岸,以中国黄、渤海沿岸的产量最大[1]。近几年,由于市场需求的不断扩大,刺参增养殖业得到了迅猛发展。同时,相应问题如自然资源匮乏、苗种质量下降、养殖病害严重等问题也暴露出来[2-3],严重制约着刺参产业的发展。通过对刺参进行遗传改良,选育出综合经济性状突出的新品种,是解决这些问题的重要途径之一。常用的遗传改良手段包括杂种优势、种间杂交和选择育种等方法。实践证明,利用选择育种的方法改良水产动物行之有效。但关于刺参选择育种的研究目前尚未见报道。

遗传参数估计是水产动物选择育种中的一项基础工作,主要用来估计育种值,制定选择指数,预测选择反应,比较选择方法以及进行育种规划[4]。动物选择育种的理论应用到水产动物上的时间较晚,始于20世纪70年代。其中鱼类的遗传参数估计研究较多,主要是以鲑科鱼和鲤鱼为主,而虾、蟹、贝类相对较少[5-8]。遗传参数估计涉及的性状参数多种多样,包括如体长、体质量、食物转化率、生长率、耗氧量和抗病力等重要的经济性状,也包括脂肪率、肉质颜色和脂肪百分率等一些肉质性状,还有一些如卵的孵化率、产卵量等繁殖性状[9-13]。由于水产动物具有高繁殖性能特性,因此遗传参数的估计方法多采用同胞分析进行估计。同胞分析所采用的方差组分估计方法,主要包括方差分析法、最小范数二次无偏估计和极大似然法[4]。中国在水产动物方面的选择育种工作开展较晚,处于起步阶段,仅见海胆(*Strongy locentrotus intermedius*)、鲤(*Cyprinus carpio*)、长毛对虾(*Penaeus penicillatus*)和罗氏沼虾(*Macrobrachium rosenbergii*)等的一些遗传参数的估计,涉及的性状主要包括如海胆的壳高、壳宽,对虾的体长、体质量等一些重要的表型经济性状[14-16]。本研究通过巢式设计的全同胞组内相关法,建立全同胞家系,通过方差分析法,对刺参耳状幼体(初耳、中耳)时期的体长遗传力进行估计,旨为刺参及水产动物的选择育种提供必要的基础依据和技术参数。

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1　材料与方法

1.1　亲本材料

32头亲本刺参(8个雄参,24个雌参)来自中国山东省烟台市海阳龙海育苗厂养殖的成体刺参群体。产卵群体养殖在温度低于18℃的虾池底部,以桡足类和硅藻为食。亲参产卵前2 h,将其运到育苗车间准备产卵。

1.2　人工授精

通常,刺参的产卵水温在18~23℃,产卵时间在20:00~24:00。选择发育良好的亲本刺参,采用阴干流水刺激(阴干45 min)和升温诱导法(较之原蓄养水温高3~5℃),促其产卵。大约在19:00,亲参开始排放精卵。一般情况下,雄参先排精,0.5 h后雌参开始排卵[1]。

每个雄参与2~3个雌参受精。取每个雌参约2×10^5粒卵子,放置于170 L的白色塑料桶内,加入适量的精液,精子的浓度维持在卵子的一个视野面上3~5个精子即可[1]。精卵在桶中混匀后,用显微镜检查受精效果。受精卵的孵化温度控制在18~23℃,孵化密度控制在10~20 mL^{-1}。

1.3　苗种培育

将构建的22个家系刺参分别放在盛有过滤海水的170 L桶中培育,水温控制在23~28℃。耳状幼体密度控制在0.5 mL^{-1}以下,每天换水2次,饵料以角毛藻和金藻为主。初耳期(受精后28 h)和中耳期(受精后第6天),每个家系分别取40~70个体,测量其体长。

1.4　统计分析

采用巢式交配设计,对于体长数据的3水平巢式不平衡方差分析通过SAS软件的GLM(General Line model)过程实现[6]。GLM过程利用最小二乘法来拟合广义线性模型,特别适合于不平衡数据的方差分析。全同胞资料表型变量的方差组成如表1所示。

表1　全同胞资料表型变量组成的方差分析

Tab.1　Analysis of variance for phenotypic variation

变异来源 Source	自由度 Degree of freedom(df)	平方和 Sum of squares(ss)	均方 Mean squares(MS)	期望均方 Expected mean squares E(MS)
雄性间　Sires	$S-1$	SS_S	MS_S	$\sigma_e^2+K_2\times\sigma_D^2+k_3\times\sigma_S^2$
雄内雌间　Dams/Sires	$D-S$	SS_D	MS_D	$\sigma_e^2+K_1\times\sigma_D^2$
雌雄内后代个体间 Progeny within sires and dams	$N-D$	SS_e	MS_e	σ_e^2
总和　Total	$N-1$	SS_T		

注:N、S、D分别为后代个体总数、雄性亲本数、雌性亲本数;σ_S^2:父系半同胞方差;σ_D^2:母系半同胞方差;σ_e^2:全同胞个体间方差。

Note: N is the number of total progeny; S is the number of sires; D is the number of Dams; σ_S^2 is the variance of paternal half-sibs; σ_D^2 is the variance of maternal half-sibs; σ_e^2 is the variance of full-sibs.

本研究为3水平经典巢式非平衡设计实验,雄性亲本内与配的雌性亲本的后代数目,每个雌性亲本的平均后代数目和每个雄性亲本后代数目都不相等,因此分别需要加权校正计算。各类别有效平均后代数目计算公式如下:

雄性亲本内与配的雌性亲本平均后代数目(K_1)、每个雌性亲本的平均后代数目(K_2)、每个雄性亲本的平均后代数目(K_3)分别按下列公式计算:

$$K_1=\frac{1}{(D-S)}\left(N-\sum_{i=1}^{s}\sum_{j=1}^{d_i}\frac{n_{ij}^2}{n_{i.}}\right)\qquad(1)$$

$$K_2=\frac{1}{(S-1)}\left(\sum_{i=1}^{s}\sum_{j=1}^{d_i}\frac{n_{ij}^2}{n_{i.}}-\sum_{i=1}^{s}\sum_{j=1}^{d_i}\frac{n_{ij}^2}{N}\right)\qquad(2)$$

$$K_3=\frac{1}{(S-1)}\left(N-\frac{1}{N}\sum_{i=1}^{s}n_{i.}^2\right)\qquad(3)$$

式中,N为后代个体总数,S为雄性亲本数,D为雌性亲本数,d_i指与第i个雄性亲本交配的雌性亲本的数目,$n_{i.}$指第i个雄性亲本后代个体数,n_{ij}指第i个雄性亲本和第j个雌性亲本后代数。

1.5　遗传力计算及其显著性检验

根据全同胞资料作二因素系统分组方差分析可以得到3个遗传力估计值[4]。

半同胞估计的狭义遗传力为半同胞组内相关系数的4倍，即：

父系半同胞

$$h_S^2=4\times\frac{\sigma_S^2}{\sigma_S^2+\sigma_D^2+\sigma_e^2}$$

母系半同胞

$$h_D^2=4\times\frac{\sigma_D^2}{\sigma_S^2+\sigma_D^2+\sigma_e^2}$$

全同胞估计的狭义遗传力为全同胞组内相关系数的2倍，即：

$$h_{SD}^2=2\times\frac{\sigma_S^2+\sigma_D^2}{\sigma_S^2+\sigma_D^2+\sigma_e^2}$$

式中，h_S^2、h_D^2、h_{SD}^2分别为父系半同胞、母系半同胞和全同胞估计的狭义遗传力，σ_S^2、σ_D^2、σ_e^2 分别为父系半同胞、母系半同胞和全同胞个体间方差。遗传力的估计值来自样本，对于其是否能够代表总体参数，需要进行显著性检验。遗传力的显著性检验采用 t 检验[4]。

2　结果

2.1 刺参耳状幼体初期和中期的体长

刺参耳状幼体初期和中期体长的平均数和标准差见表2。

2.2　刺参体长的方差分析

刺参耳状幼体初期和中期体长资料的方差分析见表3。方差分析表明，雄性亲本间和雄内雌间初耳期和中耳期幼体体长的 F 检验 P 值均小于0.01，差异极显著。

表2　刺参耳状幼体初期和中期体长的基本统计参数

Tab.2　Basic statistics on body length of *A.japonicus* Selenka at auricularia larva stage

耳状幼体时期 Larva phase	个体数 Sample nos.	平均体长/μm Mean body length	标准差 SD
初期 Initial phase	1 278	329.69	35.15
中期 Middle phase	1 031	724.43	69.38

表3　刺参初中耳期表型变量组成的方差分析

Tab.3　Analysis of variance for components of phenotypic variation of *A.japonicus* Selenka at auricularia larva stage

变异来源 Source of Variance	体长 Body length		
	自由度 Freedom	均方 Mean square	均方比 F
耳状幼体初期 Initial larva phase			
雄间 Within sires	7	54 427.688 4	71.13**
雄内雌间 Dams within sires	14	16 859.552 0	22.03**
雌雄内全同胞间 Full-sibs within sires and dams	1 256	765.148	
总和 Total	1 277		
耳状幼体中期 Middle larva phase			
雄性间 Within sires	7	194 750.206	65.15**
雄内雌间 Dams within sires	14	68 558.707	22.93**
雌雄内全同胞间 Full-sibs within sires and dams	1 009	2 989.390	
总和 Total	1 030		

注：**表示差异极显著（$P<0.01$）.

Note: ** means that difference is very significant($P<0.01$).

刺参耳状幼体初期，雄性亲本和雌性亲本间的有效平均后代数目计算结果：雄性亲本内与配的雌性亲本平均后代数目（K_1）为57.879，每个雌性亲本的平均后代数目（K_2）为58.429，每个雄性亲本的平均后代数目（K_3）为159.104。

刺参耳状幼体中期，雄性亲本和雌性亲本间的

有效平均后代数目修正结果:雄性亲本内与配的雌性亲本平均后代数目(K_1)为55.947,每个雌性亲本的平均后代数目(K_2)为43.615,每个雄性亲本的平均后代数目(K_3)为146.184。

2.3　表型变量的原因方差组分

方差分析结果与期望均方的方差组分构成,可以建立由全同胞和半同胞协方差估计各个原因差组分的对应关系,依据关系见表4。表4中列出了雄性亲本,雌性亲本和雄雌内全同胞间组分的方差,其中雌性亲本的方差大于雄性亲本的方差,表明雌性亲本间半同胞个体具有较大的变异程度,存在着较大的母性效应。

2.4　刺参耳状幼体体长遗传力的估计

依据表5父系半同胞、母系半同胞和全同胞的方差组分,估计了刺参耳状幼体初期和中期的遗传力。耳状幼体初期体长遗传力的估计值在0.74~0.87;耳状幼体中期体长遗传力的估计值在0.75~0.92。耳状幼体初中期体长遗传力显著性 t 检验结果为:依据父系半同胞、母系半同胞方差组分估计的遗传力达到显著水平,依据全同胞方差组分估计的遗传力达到极显著水平。表5也表明刺参耳状幼体初期和耳状幼体中期3个遗传力的估计值是有差别的。其中以母系半同胞遗传力估计值最高,全同胞遗传力估计值次之,父系半同胞的遗传力为最低。这与表4中方差组分的计算结果相一致。

表4　表型变量的原因方差组分

Tab.4　Analysis results of causal components of phenotypic variance

方差组分 Component of variance	体长 Body length	
	耳状幼体初期 Initial stage of auricularia	耳状幼体中期 Middle stage of auricularia
σ_S^2	235.157 9	962.105 5
σ_D^2	278.069 8	1 171.998 5
σ_e^2	765.148 0	2 989.390 0
$\sigma_P^2=\sigma_S^2+\sigma_D^2+\sigma_e^2$	1 278.375 7	5 123.494 0
$\sigma_S^2+\sigma_D^2$	513.227 7	2 134.104 0

表5　刺参耳状幼体初中期体长遗传力及其 t 检验

Tab.5　Heritabilities of body length of *A. japonicus* Selenka and its t test at auricularia larva stage

遗传力估计项目 Estimation method of heritability	耳状幼体初期 Initial stage of auricularia		耳状幼体中期 Middle stage of auricularia	
	体长 Body length	t	体长 Body length	t
父系半同胞 Paternal half-sib	0.735 6	2.455 9*	0.751 1	2.048 9**
母系半同胞 Maternal half-sib	0.870 0	2.525 4*	0.915 0	2.242 9*
全同胞 Full-sib	0.802 8	2.620 5**	0.833 1	2.585 1**

注:"*"和"**"分别表示差异显著($P<0.05$)和极显著($P<0.01$)。

Note: "*" means that difference is significant($P<0.05$); "**" means that difference is very significant($P<0.01$).

3　讨论

本研究中遗传力的3个估计值中,以父系半同胞估计的遗传力较为准确。根据母系半同胞估计得到的遗传力估计值明显大于其他两个遗传力估计值(表4),其方差也大于父系半同胞的方差,表明母系半同胞间存在较大的变异,可能存在母性效应,因此其遗传力估计值较真值偏高。据此可以认为,父系半同胞估计的遗传力是刺参幼体体长遗传力的无偏估计。

实验中估计的刺参耳状幼体初期和中期体长的狭义遗传力分别在0.74~0.87和0.75~0.92内。经统计检验,均达到显著或极显著水平。在水产动物选择育种中,利用全同胞组内相关法或者半同胞组内相关法已经获得了虾夷马粪海胆(*S. intermedius*)、牡蛎(*C. virginica*)幼体、硬壳蛤(*M. mercenaria*)、淡水虾(*M. rosenbergii*)、凡纳对虾(*P. vannamei*)和红额角对虾(*P. stylirostris*)的生长率遗传力[18-21]。已经报道的这些水产动物生长率的遗传力估计值在0.2~0.7。相比之下,刺参耳状幼体体长具有较高的遗传力。一般认为,基于全同胞组资料估计的遗传力,由于包含显性效应和母性效应,较真值偏大[4];其次,由于刺参耳状幼体初期和中期处于幼体发育的早期,其母性效应的影响也是

遗传力估计值较大的原因之一。Kanis 等[22]估计了虹鳟(*Oncorhynchus mykiss*)未发眼卵、发眼卵和仔鱼死亡率的母系半同胞遗传力,其估计值分别为0.86、0.27 和 0.06,呈现逐渐降低的趋势,表明随着胚胎的发育和孵化,其母性效应也在逐渐降低。Ayles[23]的研究结果也表现了与此相同的趋势。据此推断,随着刺参幼体的不断发育,其体长或者是其他表型性状的遗传力会逐渐降低,从而降至与其他水产动物生长性状遗传力的估计值相符合的范围内。对刺参选择育种的进一步研究,应该首先确定耳状幼体初、中期以后各个发育阶段的遗传力估计值,为育种方案的确定提供基础参数。遗传力的估计,可以考虑采用更为精确的约束最大似然法(restricted maximum likelihood, REML)。REML 作为方差组分估计方法,在样本较大时,具有渐进无偏性和样本有效性,估计的遗传力更接近真值,是目前动物育种遗传参数估计中比较理想和常用的方法[24]。

本研究结果表明,基于刺参耳状幼体体长的加性遗传方差较大,选择育种对于刺参幼体早期生长的改良具有较大的潜力。

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Heritability of auricularia larval body length for sea cucumber *Apostichopus japonicus* Selenka

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Abstract: Sea cucumbers belong to the phylum Echinodermata, class Holothuroidea. The temperate species, *Apostichopus japonicus* Selenka, naturally distributed in Bohai Bay and the Yellow Sea, is the most valuable due to its nutritional and supposed medicinal properties. With the rapid expansion and intensification of sea cucumber farming, various questions such as diseases, bad quality of larvas and less natural resources, have occurred and been serious, causing economic losses. They have become the limiting factors in the sustaining development of this industry. At last, these questions are resolved by provided excellent breeds provided by using the selecting breeding program. Before selection program can be started, breeding objectives must be defined exactly. In most species, growth traits were as the important economic traits. In the breeding program, heritability is the most basic parameter for the estimate of breeding value and selecting index, the establishment of breeding plan. In this paper, body length heritability of sea cucumber auricularia larval was estimated by means of intra group correlation of full-sib. A total of 30 maturing sea cucumber were from the population cultured. Eight sires and twenty two dams were mated by an unbalanced nest design. Each sire was mated to two or three dams, producing 8 half-sib groups and 22 full-sib families. Each full-sib family was reared separately and all families were given as equal environmental conditions as possible. The sea cucumber larvas were assessed for body length at initial stage and middle stage of auricularia (40－70 inds. for each family). Causal components of phenotypic variance were calculated with the GLM procedure of the SAS software. Analysis of variance demonstrated great differences in body length of larvas from different females mated with the same male and between males. This result also showed that the significant maternal effect was present because paternal genetic variance was significantly more than maternal genetic variance. Heritabilities in narrow sense of paternal half-sib and maternal half-sib and full sib of body length of initial and middle stage auricularia were 0.7356, 0.8700, 0.8028 and 0.7511, 0.9150, 0.8331, respectively. Hence, it was concluded that the heritability estimates (0.74,0.75) obtained from intra group correlation of paternal half-sib were precise and unbiased for body length of auricularia at initial stage and middle stage. Estimates of heritabilities in the narrow sense generally ranged from 0.2－0.7 in most marine fish and shellfish species. In our study, the estimates of heritabilities in the narrow sense for body length at initial and middle stage ranged from 0.74－0.75, larger than those reported for other marine species. It is well known larger heritability could be estimated by the full-sib intra-group correlation analysis because it included maternal effect and dominant effect. The development stage of sea cucumber was also one important factor for the exact estimate of heritability. The larger heritability would be estimated at the juvenile stage because larval growth was affected by the maternal effect. With the development of the sea cucumber, smaller heritability would be estimated due to less maternal effect. The estimated heritability indicated significant additive variation for body length at the initial and middle stage of auricularia. It was suggested that the effect for improvement through selection was particularly good for body length at auricularia larva stage of sea cucumber. [Journal of Fishery Sciences of China,2006,13(3):378－383]

Key words: *Apostichopus japonicus* Selenka; heritability; full-sib; half-sib; body length

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