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Analysis of fluctuating asymmetries in marine shrimp *Litopenaeus schmitti* (Decapoda, Penaeidae)

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Abstract. Fluctuating asymmetries (FA) are associated to instability in organism development caused by environmental and genetic factors that act during the first stages of ontogenesis. Analysis of bilateral morphometries in commercial Penaeidae stocks has shown a high AF frequency in stocks submitted to several generations in captivity. With the objective of determining a basal level of fluctuating asymmetries found in natural populations of the *Litopenaeus* genus and determine which segments are most informative in the expression of these asymmetries, 18 parameters were measured obtained from 15 bilateral segments of a sample of 40 specimens of *L. schmitti* collected along the coast of Rio Grande do Norte state, northeastern Brazil. The analysis indicated the presence of asymmetries in 27.7% of the segments measured, corresponding to segments of the pereiopods. The fluctuating asymmetries indexes observed are significantly smaller than those shown in captive stocks of *L. vannamei*, under high density and endogamy. Low fluctuating asymmetry indexes suggest an active role of the stabilizing selection in this natural population.

Key words: bilateral asymmetries, Crustacea, carciniculture, developmental instability.

Resumo. Determinação da assimetria flutuante no camarão marinho *Litopenaeus schmitti* (Decapoda, Penaeidae). Assimetrias flutuantes (AF) estão associadas à instabilidade no desenvolvimento de organismos em decorrência de fatores genéticos e ambientais que agem durante os primeiros estágios da ontogênese. Análises da morfometria bilateral em estoques comerciais de Penaeidae têm mostrado uma alta freqüência de AF em estoques submetidos a várias gerações de cultivo. Com o objetivo de determinar o nível basal de assimetria flutuante em populações naturais de espécies do gênero *Litopenaeus* e determinar quais segmentos são mais informativos na expressão destas assimetrias, 18 parâmetros foram mensurados, obtidos de 15 segmentos bilaterais de uma amostra de 40 espécimes de *L. schmitti* coletados ao longo da costa do Rio Grande do Norte, nordeste do Brasil. As análises indicaram a presença de assimetrias em 27,7% dos segmentos mensurados, correspondendo aos segmentos dos pereiópodos. Os índices de AF observados são significativamente menores que aqueles apresentados por estoques cativos de *L. vannamei*, sob intenso confinamento e endogamia. Os baixos valores de AF sugerem um papel ativo da seleção estabilizadora na população nativa desta espécie.

Palavras-chave: Crustacea, carcinicultura, instabilidade do desenvolvimento, assimetria bilateral.

Introduction

The white shrimp, *Litopenaeus schmitti* (Pérez-Farfante & Kensley 1997), is distributed in the Western Atlantic from the Antilles to the extreme south of Brazil and is found inhabiting localities up to 47 m deep (Pérez-Farfante 1970). Marine shrimp cultivation is one of the most important activities in economy of several countries.

Because of this, various genetic and morphological data need to be obtained in *L. schmitti* stocks, an important cultivated native species in Brazil.

Fluctuating asymmetry frequencies have been used extensively as an indicator of the quality of ontogenetic development in many species. It can be translated as morphological reflex to disturbances, either genetic or environmental in natural conditions (Rayman & Utter 1987, Parsons 1990, 1992, Sarre *et al*. 1994, Houle 2000), identified by measuring of bilateral traits.

The determination of the fluctuating asymmetry indexes under different conditions, especially involving Penaeidae species, performs an important function because they are very practical for monitoring the quality of native and/or exotic stocks. Fluctuating asymmetry studies on *L. vannamei* under different generations of cultivation identified a high degree of asymmetry in stocks, possibly linked to the existence of extensive endogamy caused by management (Silva 2001).

The basal fluctuating asymmetry values are not yet known in any natural stocks of *Litopenaeus* species without environmental or genetic stress. Thus the present study aimed to determine for the first time the FA levels in a wild population of a representative of the genus, *L. schmitti*, native to the Brazilian coast under natural selection, by analysis of the measure means obtained in segments of locomotors appendix pairs and establish the sex interaction.

Material and Methods

A sample of forty *L. schmitti* individuals (20 males and 20 females) were collected using trawling nets along the shore in the Baía Formosa beach (6º 22' 10" S, 35º 00' 28" W), Rio Grande do Norte state, Northeast Brazil. After collection, the animals were stored at -20^{o}C until measurement.

To establish comparison with previous data obtained for *L. vannamei,* the following measurements were chosen for analysis: length of ischium (I), mero (M), carpo (C), and propod (P) of the three first pairs of pereiopods and scaphocerytes (S) and the length and width of the side and median uropods (UL and UM). The appendixes were carefully dissected, spread out on a flat surface and measured with one replication, using a digital caliper (precision 0.01 mm) under a stereomicroscope.

Two methods of analysis were used to estimate the fluctuating asymmetries. The first consisted of the analysis of multivariate variance with repeated measurements, considering the effects of the sex, segment and side factors. Another approach was the use of the method to estimate the fluctuating asymmetry established by Palmer & Strobeck (1986) represented by the formula $FA_i=R_i-L_i/(R_i+L_i/2)$ indicated by eliminating the influence of individual size from the segment analyzed, where R_i is the mean of the right side and *Li* is the mean of the left side. The mean of the two measurements of each individual was calculated and the Multivariate analysis of variance (MANOVA) (significant at $p < 0.05$) test was applied to repeated data on the response vector formed by the 10 pairs of means obtained.

Results

Effects and interaction among the sex, segment and side factors. The analyses of the segments from the 1st, 2nd and 3rd pereiopods, scaphocerytes and uropods (analyzed jointly) indicated a significant effect for segment and sex parameters and depending on the segment, a significant or discrete interaction between them. The side factor showed no significant effect or interaction with the other factors, indicating the possibility of analysis of fluctuating asymmetry. Regarding the third pair of pereiopods the interaction of the variables side and segment presented a result fairly close to the level of significance ($p = 0.0541$; Table I). In this case, there was an indication that the variables sex and side may influence the segment size but the other interaction did not present a significant effect.

Effects and interactions between sex and segment, using weighted fluctuating asymmetries. When the same methodology was applied to the weighted fluctuating asymmetry means the effect of size was eliminated from all the segments (Table II), and the non significant effects of the factors sex, segment and the their interaction were observed, indicating the possibility of analysis of the occurrence of fluctuating asymmetries regardless of sex.

Statistics of the fluctuating asymmetries distribution in the segments. Table III shows the kurtosis for all the segments. In the first pair of pereiopods, the distributions of the mero and carpo segments presented significant asymmetry but bimodality (antisymmetry) was not detected. This fact invalidated the hypothesis of normality of the distributions confirmed in the Kolmogorov-Smirnov and Lilieffors tests. It was ascertained in the second pair of pereiopods that the mero segment presents cryptic level of asymmetry ($p = 0.0589$) in its distribution, however it is significant in the propod segment. The mero, carpo and propod segments of the third pair of pereiopods also showed significant values. The analysis carried out on the scaphocerytes indicated that the width and length parameters showed significant effect by their isolated estimative suggesting that fluctuating asymmetries can be analyzed without considering the sex. The fluctuating asymmetries distribution and the kurtosis obtained for the uropods revealed significant values. All the distributions for kurtosis were leptokurtic.

Fluctuating asymmetries by appendixes. Table IV shows the distribution normality by the Kolmogorov-Smirnov and Lilliefors test. On the 1st and 2nd pair of pereopods normality was shown in the distributions of the propod, ischium and mero, respectively, and the others were rejected. On the third pair of pereopods the ischium and mero showed normal distribution. In the median and side scaphocerytes and uropods, the Kolmogorov-Smirnov and Lillieffors normality test rejected the distribution of the width and length means. There was no indication of other forms of asymmetry in any of the segments analyzed where normality was rejected.

The results presented in Table IV show that only 27.7% of the segments studied expressed fluctuating asymmetries although 67.7% had significant effects.

Table I. Test of effects and interactions among the sex, segment and side factors of *Litopenaeus schmitti* by MANOVA with repeated measurements, to compare means of the different segments.

Fators	Factors Effects		Experimental Error			
	D.F.	M.S	D.F.	M.S	*F*	*p*
1st Pereiopod Segment	3	138.5485	114	0.2978	465.2488	0.0000*
Sex	1	77.7461	38	6.8259	11.3899	0.0017*
Side	1	0.0167	38	0.0086	1.9385	0.1719NS
Sex X 1st Pereiopod Segment	3	0.7078	114	0.2978	2.3767	0.0736
2nd Pereiopod Segment	3	672.2859	114	0.5321	1263.4208	0.0000*
Sex	1	176.2695	38	12.8097	13.7606	0.0007*
Side	1	0.0017	38	0.0049	0.3426	0.5618NS
Sex X 2nd Pereiopod Segment	3	7.1315	114	0.5321	13.4021	0.0000*
3rd Pereiopod Segment	3	2740.2278	114	1.7819	1537.8445	p<0.0001*
Sex	1	246.0827	38	25.7700	9.5492	0.0037*
Side	1	0.0002	38	0.0011	0.1720	0.6806 NS
Segment x Side	3	0.0059	114	0.0023	2.6222	0.0541
Sex X 3rd Pereiopod Segment	3	17.2367	114	1.7819	9.6734	p<0.0001*
Scaphoceryte	1	6492.8135	38	2.1576	3009.2852	0.0000*
Sex	1	123.2888	38	11.7025	10.5352	0.0024*
Side	1	0.0018	38	0.0024	0.7524	0.3912 NS
Sex X Scaphoceryte	1	27.7889	38	2.1576	12.8796	0.0009*
Uropod	3	4822.9624	114	2.0075	2402.4592	0.0000*
Sex	1	172.2464	38	17.2538	9.9831	0.0031*
Side	1	0.0025	38	0.0277	0.0905	0.7651 NS
Sex X Uropod	3	19.9961	114	2.0075	9.9606	0.0000*

NS - not statistically significant; * - statistically significant

Discussion

The level of fluctuating asymmetries can be estimated from the analysis of bilateral appendixes of individuals in natural populations revealing valid data on environmental and genetic stability to which that group is submitted. Although fluctuating asymmetry has been used successfully in plants and animals (Galhardo 1995, Evans & Marshall 1996, Møller *et al*. 1999), there are few reports of its use in marine shrimps (Clarke 1993, Silva 2001).

Asymmetries presenting heredity components, such as directional asymmetry and antisymmetry, can harm fluctuating asymmetry analysis (Palmer & Strobeck 1992). However, analyzes carried out on *L. schmitti* did not show the presence of either of these asymmetries in spite of the heterogeneity in the size of the individuals. This variability in size of individuals motivated the use of relative fluctuating asymmetry formula (Palmer & Strobeck 1986). In the two forms of analysis applied to the data, the occurrence of fluctuating asymmetries could be observed, a situation previously identified in *L. vannamei* (Silva 2001).

An important question in the study of fluctuating asymmetries is the choice of the structures to be used. In shrimp, the reduced size of the appendices and ill-defined landmarks can favor imprecise results significantly. For this reason, the rigid pereiopod, scaphoceryte and uropod segments were chosen in this study, in detriment to membranous structures such as pleopods, whose measurement is less accurate (Silva 2001).

Table II. Test of effects and interaction among the factors sex and segments of *Litopenaeus schmitti*, by MANOVA with repeated measurements using weighted fluctuating asymmetries as response.

Factors	Factors Effects		Experimental Error			
	D.F	M.S	D.F	M.S	*F*	*p*
Sex	1	0.0010	38	0.0006	1.6190	0.2110^{NS}
1st Pereiopod Segments	3	0.0003	114	0.0003	1.0589	0.3695^{NS}
Sex X 1st Pereiopod Segment	3	0.0001	114	0.0003	0.3623	0.7803^{NS}
Sex	1	0.000005	38	0.0002	0.0305	0.8622^{NS}
2nd Pereiopod Segment	3	0.000017	114	0.0002	0.1064	0.9562^{NS}
Sex X 2nd Pereiopod Segment	3	0.000061	114	0.0002	0.3894	0.7608^{NS}
Sex	1	0.00005	38	0.00002	2.7530	0.1053 ^{NS}
3rd Pereiopod Segment	3	0.00009	114	0.00004	2.0241	0.1145 ^{NS}
Sex X Segment	3	0.00001	114	0.00004	0.2957	0.8284 ^{NS}
Sex	1	0.00012	38	0.00005	2.4695	0.1244 ^{NS}
Scaphoceryte	1	0.00038	38	0.00014	2.7020	0.1085 ^{NS}
Sex X Scaphoceryte	1	0.00034	38	0.00014	2.4242	0.1278 ^{NS}
Sex	1	0.00000	38	0.00020	0.0017	0.9676 ^{NS}
Uropods	3	0.00057	114	0.00127	0.4508	0.7172 ^{NS}
Sex X Uropods	3	0.00175	114	0.00127	1.3819	0.2519 ^{NS}

NS - no statistically significant; * - statistically significant

The pereiopods perform the functions of food manipulation, locomotion and defense. While the scaphocerytes act in feeding, the uropods are used for defense and swimming (Narchi 1973). These appendixes and segments of the crustaceous can show some degree of variability. A morphometric study on the pink Mediterranean shrimp, *Aristeus antennatus*, showed that the scaphocerytes, uropods and the carpo of the third pair of pereiopods show adaptive plasticity (Sardà *et al*. 1998).

Structures with large functional importance are normally subject to strong selective pressure in natural populations. Thus the presence of the significant fluctuating asymmetry indexes in such structures may reflect the maximum degree of tolerability permitted by environmental pressures.

Characteristics with weak stabilizing selection are less stable and therefore can develop a wide range of phenotypes and show high levels of fluctuating asymmetry (Balmford *et al*. 1993). This can result in the characteristics that are functionally important presenting extremely restricted development ways, revealing lower fluctuating asymmetry levels (Møller & Swaddle 1997, Kodrick-Brown 1997). In birds, the wings have more stable development than the tails due to their greater aerodynamic importance (Møller & Höglund 1991, Balmford *et al*. 1993, Anciães 1998). Apparently a similar situation was identified here among the pereiopods and uropods in *L. schmitti* with marked asymmetries in the first and absence of asymmetries in the latter. But the hypothesis cannot be disregarded that structures with segments in series such as the pereiopods can suffer a greater degree of asymmetry during development than simpler structures such as the uropods and scaphocerytes.

The level of asymmetry fluctuates within populations (with approximately normal distribution) indicating that is a property of the population. Some individuals tend to present some level of asymmetry that reflects how much its genotype can express the ideal phenotype in given conditions. This can lead to rejection of the normal distribution, although the segment analyzed is statistically significant (Galhardo 1995), as observed in all the *L. schmitti* appendixes and segments.

Thus, considering the fluctuating asymmetry properties (Palmer & Strobeck 1992, Møller 1997), the occurrence of fluctuating asymmetries could only be identified in the propod (1st pair), ischium (2nd and 3rd pairs) and mero (2nd pair) segments. For the other segments the pereiopods and the measurements (width and length) of scaphocerytes (WS and LS) and of lateral and medial uropods (WLU, *width of lateral uropod*, LLU, *length of lateral uropod*, WMU, *width of medial uropod*, LMU, *length of medial uropod*) fluctuating asymmetry was not considered to exist because it did not fit in fluctuating asymmetry properties.

Markow (1995) considered fluctuating asymmetries as a random flight from a predicted bilateral symmetry, so that one group of differences between the sides creates a normal distribution. One level of fluctuating asymmetries that is relatively higher than the level found in an appropriate control group reflects the reduced homeostasis of development. Bearing in mind the optimum environmental conditions available for *L. schmitti*, the reduced fluctuating asymmetry indexes might be considered as base levels of the population. Given the phylogenetic proximity with congeneric species, these data could be a comparative parameter for others penaeid species, populations or cultived stocks.

Table III. Statistics of the fluctuating asymmetry distribution in the segment measurements (ischium, mero, carpo and propod) in *Litipenaeus schmitti*

Segments	Average	Confidence Interval 95%		Asymmetry Coefficient	*p* asymmetry	Kurtosis Coefficient	*p* Kurtosis
		Low range	High range				
1st pereiopod							
I	0.0009	-0.0087	0.0104	-0.3356	0.3806NS	8.7194	p<0.0001*
M	-0.0025	-0.0055	0.0006	-3.6569	p<0.0001*	17.5976	p<0.0001*
C	-0.0055	-0.0120	0.0009	-2.9157	p<0.0001*	9.0407	p<0.0001*
P	-0.0014	-0.0033	0.0005	-0.6713	0.0884NS	2.0727	0.0107*
2nd pereiopod							
I	-0.0007	-0.0062	0.0048	-0.1831	0.6299NS	5.4760	p<0.0001*
M	0.0000	-0.0024	0.0024	-0.7511	0.0589NS	7.2738	p<0.0001*
C	-0.0014	-0.0057	0.0030	0.6367	0.1048NS	7.9385	p<0.0001*
P	-0.0001	-0.0029	0.0028	-2.2742	p<0.0001*	12.2844	p<0.0001*
3rd pereiopod							
I	-0.0008	-0.0031	0.0015	-0.1362	0.7196 NS	-0.1693	0.8197 NS
M	0.0013	-0.0003	-0.0003	0.9157	0.0242*	2.6072	0.0021*
C	-0.0011	-0.0025	0.0004	-1.4651	0.0009*	6.7600	p<0.0001*
P	0.0020	-0.0003	0.0042	2.6668	p<0.0001*	9.6223	p<0.0001*
Scaphoceryte							
WS	-0.0027	-0.0068	0.0014	-1.3319	0.0021*	8.4406	p<0.0001*
LS	0.0016	-0.0002	0.0035	1.6978	0.0002*	3.6421	p<0.0001*
Uropods							
WLU	-0.0028	-0.0067	0.0012	-2.3601	p<0.0001*	7.4722	p<0.0001*
LLU	-0.0033	-0.0169	0.0103	-4.6449	p<0.0001*	28.8452	p<0.0001*
WMU	0.0005	-0.0070	0.0080	2.8156	p<0.0001*	13.3322	p<0.0001*
LMU	0.0049	-0.0076	0.0174	4.8598	p<0.0001*	29.1741	p<0.0001*

NS- no statistically significant; * - statistically significant; Assimetry coefficient – differences between left (-) and right (+) sides; WS – width scaphoceryte; LS – length scaphoceryte; WLU- width lateral uropod; LLU – length lateral uropod; WMU- width medium uropod; LMU- length medium uropod.

Table IV. Presence of fluctuating asymmetries (FA) in the parameters measured in each appendix of *Litopenaeus schmitti* specimens.

Appendix	Segments	Average	*p*	K - S	Results
1st pereiopod	I	0.0009	0.3806NS	-	~FA
	M	- 0.0025	p< 0.0001*	-	~ FA
	C	- 0.0055	p< 0.0001*	-	~ FA
	P	- 0.0014	0.0884NS	+	FA
2nd pereiopod	I	- 0.0007	0.6299NS	+	FA
	M	0.0000	0.0589NS	+	FA
	C	- 0.0014	0.1048NS	-	~ FA
	P	- 0.0001	p<0.0001*	-	~ FA
3rd pereiopod	I	- 0.0008	0.7196NS	+	FA
	M	0.0013	0.0242*	+	FA
	C	- 0.0011	0.0009*	-	~FA
	P	0.0020	p< 0.0001*	-	~FA
Scaphoceryte	WS	- 0.0027	0.0021*	-	~FA
	LS	0.0016	0.0002*	-	~FA
Uropods	WLU	-0.0028	p< 0.0001*	-	~FA
	LLU	-0.0033	p< 0.0001*	-	~FA
	WMU	0.0005	p< 0.0001*	-	~FA
	LMU	0.0049	p< 0.0001*	-	~FA

NS - not statistically significant; * - statistically significant; K-S – Kolmogorov-Smirnov test; (+) normal; (-) not normal; ~ despite statistically significant were rejected the FA; I –ischium; M – mero; C – carpo; P – propod; WS – width scaphoceryte; LS – length scaphoceryte; WLU - width lateral uropod; LLU – length lateral uropod; WMU - width medium uropod; LMU - length medium uropod.

The distribution of differences between the left and the right sides measures presented leptokurtic distribution, indicating FA (Møller 1996). The preponderance of the leptokurtic distribution presented in results is consistent with some models presented (Møller 1997, Vøllestad *et al*. 1999) showing that the differences inherent to ability of individuals control the development process invariably implies this type of distribution.

The comparative FA study in *L. schmitti* revealed the occurrence of fluctuating asymmetries is in a non preferential form between the sexes. These results differ from those obtained with stocks of *L. vannamei* (Silva 2001) whose females were more asymmetric than males.

For various authors (Jones 1987, Thornhill 1992, Möller 1995), natural selection acting on morphological characteristics such as the sensor pores and the number of rays in fish fins would act equally in males and females since less stable genotypes would have less survival. The effect of stabilizing selection on fluctuating asymmetries in a *Cyprinodon pecosensis* population influenced the degree of fluctuating asymmetry of the characteristic in both sexes as well as in the reduction of its variability indicating that the modal phenotypes would be more symmetrical than those more extreme, suggesting that the individuals with values close to the mean of the group represent highly stable genotypes (Kodric-Brown & Hohmann 1990, Kodric-Brown 1997).

The low indexes of fluctuating asymmetries obtained for the natural *L. schmitti* population showed the stability of the population in the face of the deviation of development, permitting the establishment of maximum tolerance values under natural conditions. These results would permit the use of this methodology to monitor other natural Penaeidae populations, and the applied use in stock control under cultivation conditions.

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