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Variation of Multivariate Allometry for Sword Prawn (*Parapenaeopsis hardwickii*) in the East China Sea and Taiwan Strait

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ABSTRACT

Multivariate allometric coefficients were estimated and compared for five female sword prawn (*Parapenaeopsis hardwickii*) samples collected separately from the north of East China Sea (NECS02) and the waters off Tamsui (Tamsui10), Taichung (Taichung11 and Taichung02), and Cheding (Cheding02). Twelve measurements were measured for each individual. The 1st eigenvector obtained from the covariance matrix of log-transformed data was used to represent the multivariate allometric coefficients. The dendrogram of five samples was constructed by using the angles between five 1st eigenvectors, and a permutation test was used to test if the difference between two multivariate allometric coefficients obtained from different samples/groups was significant. Five samples were clustered into three distinct groups, the group 1 included NECS02, the group 2 included Tamsui10 and Taichung11, and the group 3 included Taichung02 and Cheding02 samples. Permutation tests indicated that the difference of each within group pairwised multivariate allometric coefficients is not significant and of each between groups pairwised multivariate allometric coefficients is significant. Therefore, we concluded that there are three different multivariate allometric patterns for sword prawns from these studied waters.

***Key words**: Parapenaeopsis hardwickii, Allometry, East China Sea, Taiwan Strait.*

INTRODUCTION

Organisms are not usually isometric (Reiss, 1989). Allometry is disproportionate growth between two body parts (Gould, 1966), and contrasts with isometric growth. Allometric analyses can assess the covariation of characters (Cock, 1966), and provide a method to elucidate the relationship between processes of growth and evolution (Blackstone, 1987). Several studies, however, support the view that allometries are not free from environmental influences but may in fact themselves respond to environmental fluctuations, such as variation in nutrition (Moczek, 2002).

Analyses for allometry have been developed for bivariate allometric equation and for a multivariate generalization of the bivariate allometric equation. The formula of bivariate allometry (Huxley, 1932) assumes a power function of the form $y = b\,x^{\alpha}$, where x and y are measurements and the constant α is often called the allometric coefficient. Jolicoeur (1963) used the 1st eigenvector extracted from the covariance matrix of log-transformed data to reflect the multivariate allometric coefficients. The multivariate allometric

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coefficients can be easily translated to bivariate allometric coefficients by using the ratio of the coefficients in the first eigenvector for 2 variables corresponding to variable in the bivariate allometric analysis (Shea, 1985).

Although patterns of morphometric variation can be studied using bivariate allometry, geographic variation is a multivariate phenomenon (Gould and Johnston, 1972), and simultaneous analysis of a representative array of characters is more likely to detect group differences (Jolicoeur and Mosimann, 1960). Multivariate allometric coefficients for comparisons among groups are also applied to some statistical methods. For example, one assumption that these groups under consideration share a common multivariate allometric pattern is a basic precondition in Burnaby's method (Burnaby, 1966), shearing principal component analysis (PCA) (Humphries *et al.*, 1981) or multiple-group PCA (Thorpe, 1988) for size correction. However, this assumption has rarely been tested (Klingenberg, 1996).

Sword prawn (*Parapenaeopsis hardwickii*) is distributed mainly in Indian-West Pacific Ocean from Pakistan to Japan and inhabits sand ground area at 5 to 90 meters water depth. This species is one of the most abundant and highly valued species in the Taiwan Strait and the East China Sea (Wu, 1985). Although several studies on the fisheries biology of sword prawn in this area have been conducted (e.g., Guo, 1993; Tzeng and Yeh, 2000; Li *et al.*, 2000; Zheng and Li, 2002), there is no information on multivariate allometry. Therefore, the objective of this study is to estimate and compare the multivariate allometric coefficients for the sword prawn in the East China Sea and Taiwan Strait.

MATERIALS AND METHODS

Five samples were respectively collected from the north of East China Sea (NECS-02) and the waters off Tamsui (Tamsui10), Taichung (Taichung11 and Taichung02) and Cheding (Cheding02) (Fig. 1) between Oct. 2002 and Feb. 2003. The symbol (sampling area suffixed a figure, e.g., Tamsui10) denoted the sampling area and month. The individuals were separated by sex. Twelve measurements were recorded on each specimen (Fig. 2). They were antennal spine width (ASW), hepatic spine width (HSW), carapace length (CL), diagonal carapace length (DCL), first abdominal segment length (1ASL), second abdominal segment length (2ASL), third abdominal segment length (3ASL), fourth abdominal segment length (4ASL), fifth abdominal segment length (5ASL), sixth abdominal segment width (6ASW), sixth abdominal segment diagonal length (6ASDL), and total length (TL). Because the sample size of male was too small to analyze, only female data was used in this study. Restricting ranges of carapaces length of samples to specific length classes was conducted in this study. The sample size, sampling area code, mean and range of carapace length are summarized in Table 1. All characters were measured to the nearest 0.01 mm except total length to the nearest 0.1 mm.

Estimation of multivariate allometric coefficients followed the recommendation of Jolicoeur (1963). The 1st eigenvector extracted from the covariance matrix of log-transformed data for each sampling area was used to represent the multivariate allometric coefficients. A bootstrap technique (Effron and Tibshirani, 1986) was used to assess the accuracy of allometric coefficients. A bootstrap sample of corresponding sample size was drawn at random with replacement. For each analysis, 10000 bootstrap iterations were performed.

The angles between five 1st eigenvectors indicate their similarity in multivariate allometric coefficients obtained from different geographic samples. The angle α was computed as the arc cosine of the inner product of the two 1st eigenvectors (Gibson *et al.*, 1984), α = arccos (B x C) x 180/π, where B and C are the 1st eigenvectors. An increasing angle indicates a decreasing simiarity. Since the orientation of PCA vector is arbitrary, the absolute

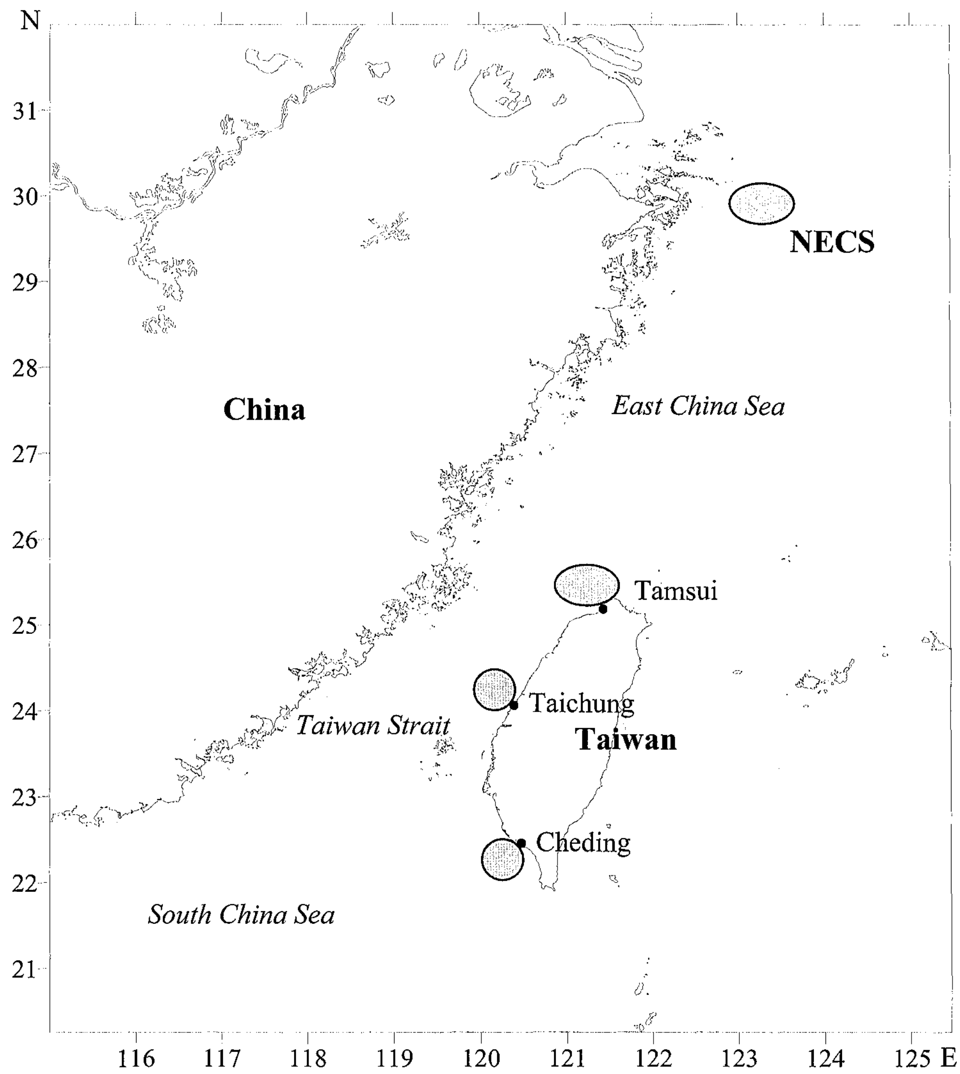

Fig. 1. The sampling areas in the East China Sea and Taiwan Strait.

value of the angle computed is used. These angles were treated as distance coefficients and used in cluster analysis. Based on these angles, the dendrogram of five samples was constructed by applying unweighted pair-group method with arithmetic means (UPGMA).

Permutation test proposed by Tzeng and Yeh (1999) was used to test if the difference between two multivariate allometric coefficients is significant. The angle between two multivariate allometric coefficients was treated as a statistic. For each permutation test, 10000 iterations were performed. The position of the angle (θ_0) estimated obtained from original data sets was determined among the ordered values of the angles (θ_1) obtained from permuted data sets. The proportion (*P*) of the observed angle values greater than or equal to θ_0 was also calculated. This *P* value can be interpreted in the same way as for conventional tests of significance: if it is less than 5% then this provides some evidence that the null hypothesis is not true, if it is less than 1% then it provides

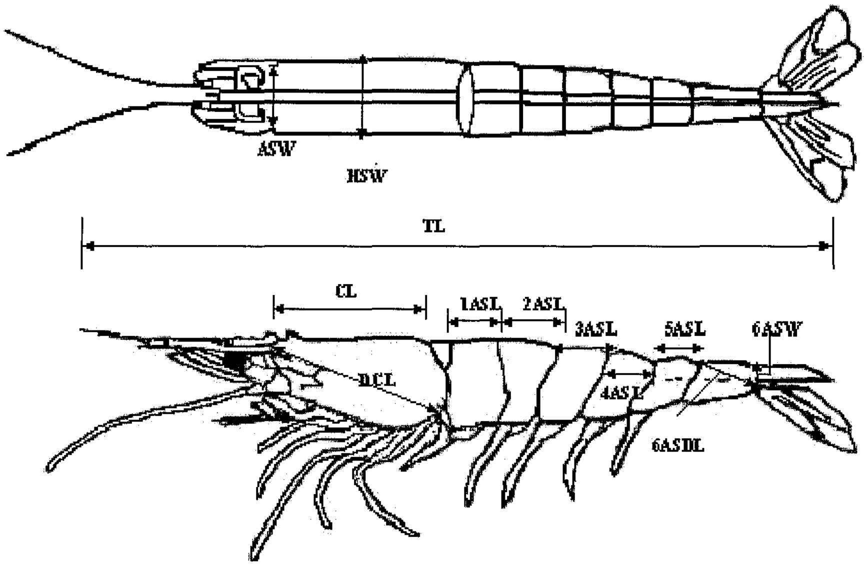

Fig. 2. Diagram of *Parapenaeopsis hardwickii* showing the body parts measured.

Table 1. Code of sampling site, sample size, sampling date, and mean, standard deviation (SD) and range of carapace length (CL, mm) for five female sword prawn (*Parapenaeopsis hardwickii*) samples in the East China Sea and Taiwan Strait. The figure in the first column represents the sampling month.

Area code	Sampling site	Sample Size	Sampling date	Mean of CL	SD of CL	Range of CL
NECS02	North of the East China Sea	552	Feb. 2003	24.34	1.69	21.08-28.93
Tamsui10	Waters off Tamsui	228	Oct. 2002	23.97	1.60	21.04-28.70
Taichung11	Waters off Taichung	240	Nov. 2002	24.58	1.66	21.33-28.94
Taichung02	Waters off Taichung	262	Feb. 2003	24.59	1.91	21.17-28.86
Cheding02	Waters off Cheding	464	Feb. 2003	24.66	2.27	21.02-28.85

strong evidence that the null hypothesis is not true (Tzeng and Yeh, 1999).

All analyses were conducted by using various algorithms programmed by IML procedure (SAS, 1985), but the dendrogram was constructed by using NTSYS-pc (Rohlf, 1987)

RESULTS

The first eigenvector and the percentages of total variance explained by the 1st eigenvalues are shown in Table 2. For every sample the first eigenvector represents the multivariate allometric coefficients. Among the five samples, all the physiological variables carry on positive loadings with little differences (Table 2). The high percentages variance corresponding to the first eigenvalues indicates that the first principal component can account for the physiological variation significantly (Table 2). The maximum percentage of total variance explained by 1st eigenvalues was 93.14% estimated from Cheding02, but the smallest one was 83.77% estimated from the Tamsui10. The estimates of multivariate allometric coefficients were considered fairly stable, as indicated by the relatively small standard deviations of the estimates.

The angles between five multivariate

Table 2. Multivariate allometric coefficients with corresponding standard deviations (in parentheses) and percentages of total variance explained by the first eigenvalues for five female sword prawn samples in the East China Sea and Taiwan Strait.

	Sample code				
Variable	NECS02	Tamsui10	Taichung11	Taichung02	Cheding02
ASW	0.2977 (0.0038)	0.2946 (0.0062)	0.2834 (0.0050)	0.3153 (0.0049)	0.3053 (0.0024)
HSW	0.3215 (0.0040)	0.3323 (0.0134)	0.3199 (0.0066)	0.3207 (0.0052)	0.3183 (0.0038)
CL	0.3127 (0.0029)	0.3215 (0.0062)	0.3131 (0.0046)	0.3191 (0.0037)	0.3215 (0.0022)
DCL	0.3126 (0.0027)	0.3170 (0.0050)	0.3080 (0.0042)	0.3134 (0.0031)	0.3165 (0.0020)
1ASL	0.3127 (0.0083)	0.2993 (0.0078)	0.2954 (0.0083)	0.2810 (0.0050)	0.2937 (0.0038)
2ASL	0.2753 (0.0045)	0.2528 (0.0086)	0.2679 (0.0084)	0.2735 (0.0071)	0.2753 (0.0035)
3ASL	0.2805 (0.0039)	0.2676 (0.0090)	0.2869 (0.0061)	0.2644 (0.0052)	0.2662 (0.0035)
4ASL	0.2719 (0.0072)	0.2798 (0.0099)	0.2836 (0.0070)	0.2614 (0.0073)	0.2776 (0.0043)
5ASL	0.3068 (0.0079)	0.2854 (0.0102)	0.2837 (0.0093)	0.2835 (0.0065)	0.2751 (0.0060)
6ASW	0.2470 (0.0072)	0.3033 (0.0149)	0.3089 (0.0092)	0.3126 (0.0093)	0.3015 (0.0052)
6ASDL	0.2609 (0.0040)	0.2351 (0.0102)	0.2533 (0.0062)	0.2616 (0.0061)	0.2604 (0.0025)
TL	0.2505 (0.0035)	0.2581 (0.0077)	0.2495 (0.0078)	0.2424 (0.0060)	0.2391 (0.0031)
% variance	86.14	83.77	87.38	89.35	93.14

Table 3. The angles (degree) between five multivariate allometric coefficients in five female sword prawn samples.

	NECS02	Tamsui10	Taichung11	Taichung02	Cheding02
NECS02	0				
Tamsui10	4.2458 (*P*=0.0003)	0			
Taichung11	4.1275 (*P*=0.0005)	2.2213 (*P*=0.4687)	0		
Taichung02	4.6716 (*P*=0)	2.9933 (*P*=0.0420)	3.2094 (*P*=0.0341)	0	
Cheding02	3.9964 (*P*=0)	2.5377 (*P*=0.0054)	2.1664 (*P*=0.0198)	1.5785 (*P*=0.1849)	0

allometric coefficients are shown in Table 3. The angle (4.6716°) between multivariate allometric coefficients obtained from NECS02 and Taichung02 samples was significantly different, but the one (1.5785°) obtained from data sets of Taichung02 and Cheding02 was most similar. The dendrogram of five samples is shown in Fig. 3. Five samples were clustered into three distinct groups; the group 1 included NECS02; the group 2 included Tamsui10 and Taichung11; the group 3 included Taichung02 and Cheding02. The results of permutation test indicated that the differences between multivariate allometric coefficients for the samples in the same group are not significant, but pairwise multivariate allometric coefficients for the samples in different groups are significantly different (Table 3).

Thus the specimens in the same group were first pooled, and then multivariate allometric coefficient was re-estimated in each group. All 1st eigenvectors have all-positive and near-equal loadings and are interpreted as representing multivariate allometric coefficients in each group (Table 4). The proportion of total variance explained by the 1st eigenvalues ranged from 86.00% to 91.94% for three different groups. These

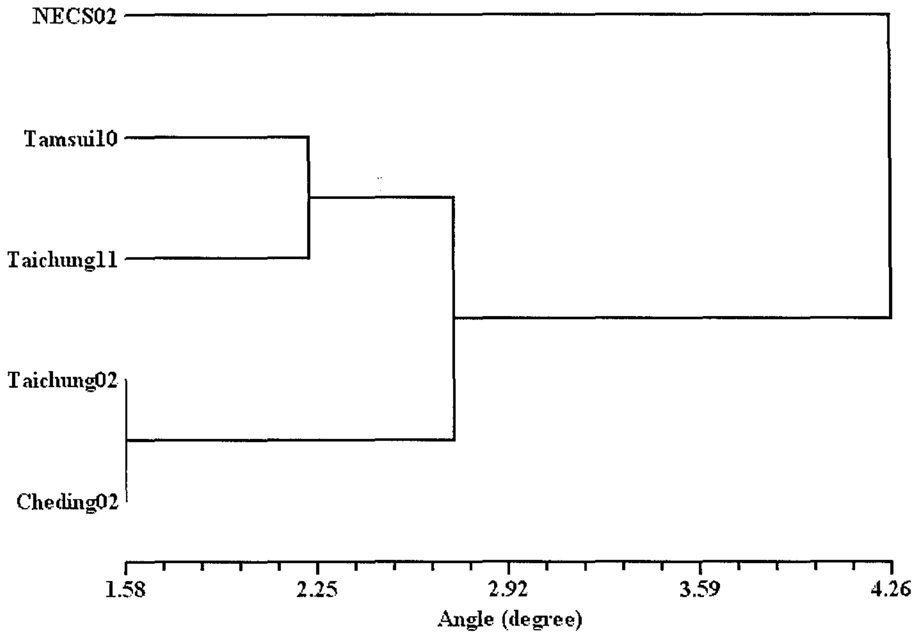

Fig. 3. Dendrogram of five female sword prawn samples.

Table 4. Multivariate allometric coefficients with corresponding standard deviations (in parentheses) and percentages of total variance explained by the first eigen-values in three different groups.

Variable	The first group	The second group	The third group
ASW	0.2977 (0.0038)	0.2896 (0.0039)	0.3082 (0.0022)
HSW	0.3215 (0.0040)	0.3285 (0.0074)	0.3184 (0.0031)
CL	0.3127 (0.0029)	0.3161 (0.0036)	0.3207 (0.0019)
DCL	0.3126 (0.0027)	0.3127 (0.0031)	0.3155 (0.0017)
1ASL	0.3127 (0.0081)	0.2952 (0.0057)	0.2903 (0.0032)
2ASL	0.2753 (0.0046)	0.2585 (0.0057)	0.2748 (0.0031)
3ASL	0.2805 (0.0039)	0.2775 (0.0052)	0.2658 (0.0029)
4ASL	0.2719 (0.0072)	0.2855 (0.0061)	0.2739 (0.0037)
5ASL	0.3068 (0.0079)	0.2850 (0.0067)	0.2775 (0.0047)
6ASW	0.2470 (0.0071)	0.2995 (0.0082)	0.3051 (0.0046)
6ASDL	0.2609 (0.0040)	0.2454 (0.0051)	0.2611 (0.0025)
TL	0.2505 (0.0036)	0.2579 (0.0054)	0.2392 (0.0029)
% variance	86.14	86.00	91.94

estimates were considered fairly stable, as indicated by the relatively small standard deviations of the estimates.

The differences between three multivariate allometric coefficients obtained from three different groups were also tested by permutation tests. The angles (θ_0) between three multivariate allometric coefficient separately derived from three different groups are shown in Table 5. The values of *Ps* are clearly smaller than 5%, so these tests are all significant. These indicated that there is a significant non-random structure in the data, and supported that the differences between multivariate allometric coefficients from

Table 5. The angles (degree) between three multivariate allometric coefficients derived from three groups.

	Group 1	Group 2	Group 3
Group 1	0		
Group 2	3.8169 (P=0)	0	
Group 3	4.1621 (P=0)	2.3777 (P=0.0002)	0

different groups are all significant.

DISCUSSION

The result of five samples were clustered into three distinct groups suggests that there might be considerable difference between multivariate allometric coefficients from different geographical populations. The permutation tests indicate it is extremely unlikely that the large angle between multivariate allometric coefficients from original data sets in different groups was due to chance. Therefore, there are three different multivariate allometric patterns in five samples.

The proportions of total variance explained by the 1st eigenvalues ranged from 83.77% to 93.14% for five samples and from 86.00% to 91.94 for three groups in this study. The majority of variance in each sample/group was explained by the first eigenvalues, which showed a good fit of the model of multivariate allometry to the data (Bjorklund, 1993).

Differences between allometric patterns are mainly derived from four sources: (1) ontogenetic variation; (2) environmental variation; (3) genetic variation; and (4) developmental noise or experimental error. However, they are both difficult to measure and intertwine for wild populations.

To elucidate the relationship between populations, the effect of growth variation within/between groups must be decreased (Bookstein *et al*., 1985). Narrowing the differences of size between samples may reduce such effects. Restricting sample comparisons to specific length classes may disregard ontogenetic change within groups, and the information may be necessary for meaningful descriptions of sample/group differences (Bookstein *et al*., 1985). However, this effect may not be serious in this study, because the carapace length of each individual in each sample/group was not all equal. It is relevant that because biological data are noisy, if the range of size included in allometric analysis is too small, the probability is high that the scaling exponent and allometric coefficient will be distorted by sampling error (LaBarbera, 1989).

Two main spawning areas were separately found in the Taiwan Strait and East China Sea. One is located in the middle and north of the Taiwan Strait (Guo, 1993), but the other is located in the north of the East China Sea (Zheng and Li, 2002). In the Taiwan Strait, two peaks of spawning season were found (Guo, 1993); one is between February and April, and the other is between October and November. In the north of the East China Sea, the spawning season lasts from May to September, with the peak usually occurring between June and July (Zheng and Li, 2002). Two environmental factors prevailing in studied waters may result in these differences. Firstly, there is relative large fresh water input (the Yangtze River) in the north of the East China Sea, and this input also supply the major source of nutrients; in the north of Taiwan Strait, there is small fresh water input (the Tamsui River), and this input also supply the major source of nutrients; in the middle and south of Taiwan Strait, there is more less fresh water input, and the major source of nutrients is from the Kuroshio. Secondly, the annual mean surface temperatures of the north of East China Sea, the waters off Tamsui, Taichung and Cheding are 20°C, 24°C, 25°C and 26°C, respectively. In the north of the East China Sea, the temperature of the sea is lower than in the Taiwan Strait. Therefore, the differences between the group 1 and group 2 or between the group 1 and group 3 are mainly derived from genetic and environmental distinctness. The mean surface temperatures of spring (March to May), summer (June to August), autumn (September to November) and winter (December to February) in the waters off Tamsui are 21°C, 28°C, 23°C and 18°C, the ones in the waters off Taichung are 23 °C, 28°C, 25°C and 21°C, and the ones in the waters off Cheding are 25°C, 30°C, 26 °C and 23°C (National Center for Ocean Research, Ocean Data Bank, http://www.ncor.ntu.edu.tw/ODBS/). Two Taichung samples were separately clustered into the group 2 and group 3, thus it may be possible that these individuals in the two stocks/populations migrate and arrive one after another to Taichung location. Therefore, we might also consider that the differences between group 2 and group3 may also be derived from genetic and environmental distinctness.

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東海及台灣海峽產劍蝦之多變量異速成長變異

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估計及比較來自於東海北部(NECS02)及淡水(Tamsui10)、台中(Taichung11 和 Taichung02)和茄定外海(Cheding02)等 4 個水域 5 個雌性劍蝦樣本之多變量異速成長係數。每個體量測 12 個外部形質，將所得之資料經對數轉換，計算其共變方矩陣，經主成份分析所得之第一特徵向量即為多變量異速成長係數。利用兩兩第一主成份向量間之角度資料，建構 5 樣本之表型圖，另利用置換排列分析法，檢定兩多變量異速成長係數間是否有顯著差異。表型圖顯示，5 樣本可分為 3 群：群 1 含 NECS02，群 2 含 TAMSUI10 和 Taichung 11，群 3 含 Taichung02 和 Chedig02 樣本。置換排列分析法檢定顯示，群內任一配對的多變量異成長係數間沒有顯著差異，但群間任一配對的多變量異成長係數間皆有顯著差異。因此，我們判定本研究水域產之劍蝦中具有三種不同多變量異速成長的型態。

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