Morphological variations of the winged pearl oyster *Pteria penguin* (Roding, 1798) from South China Sea

HUAYANG GUO*, DIANCHANG ZHANG, SHIGUI JIANG, YOUNING LI, NAN ZHANG, YU WANG AND ZHENHUA MA*
South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou - 510 300, P. R. China
*Key Laboratory of South China Sea Fishery Resources Exploitation and Utilisation, Ministry of Agriculture, Guangzhou - 510 300, P. R. China

*e-mail: zhenhua.ma@hotmail.com

ABSTRACT

The present study was undertaken to evaluate the morphological variations of *Pteria penguin* (Roding, 1798) in wild as well as cultured populations from South China Sea. A total of 307 samples were collected from five different geographic locations comprising three wild (Pop. 1, 2 and 4) and two cultured (Pop. 3 and 5) populations and 10 measured traits were analysed. Principal component analysis (PCA), discriminant analysis and cluster analysis were used to evaluate the morphological variations in the collected samples. Results showed a low intra-population variation within the five sampled populations. Multivariate analyses indicated that the five populations were more or less differentiated on the basis of body characters, particularly those related to major dimensions of the shell outline and their ratios. Discriminant analysis revealed that the overall random assignment of individuals into their original groups was high (81.8%), indicating that these populations are highly divergent from each other. The proportion of individuals correctly classified into their original groups was 96.9, 76.7, 75.0, 78.0 and 82.0% for populations 1, 2, 3, 4 and 5 respectively. Cluster analysis showed highest morphological variation between Pop. 1 and Pop. 2. All other populations (Pop. 3, Pop. 4 and Pop. 5) were found to be morphologically similar and consistent with the respective geographical location. Results of the present study will be of use in resource assessment and management of *P. penguin* in the South China Sea.

Keywords: Geographical populations, Morphometric variation, Multivariate analysis, *Pteria penguin*

Introduction

Morphological variation is considered as one of the basic characteristics to assess the population differences in aquatic organisms. Measurement, description and analysis of the morphological variations are fundamental steps to answer questions of biological adaptability (Ge and Hong, 1995). Due to genetic differences or environmental factors, morphological characters of aquatic animals are often varying along with geographic gradient among wide-ranged coastal marine animals (Tzeng et al., 2001; O’Reilly and Horn, 2004; Murta et al., 2008). Intra-specific variation in animals is usually regarded as the adaptive mechanism to different environments (Orensanz et al., 1991; Cadrin, 2000; Tzeng et al., 2001; Marquez et al., 2010). Studies on the morphological variations of target species can reveal the dynamics of populations and such information can be used to design management strategies (Orensanz et al., 2005). As one of the solid evaluation parameters, morphological variation has been widely used in population studies (Murta, 2000; Tzeng et al., 2001; Chen et al., 2010), stock discrimination (Cadrin et al., 2005; Turan et al., 2006; Murta et al., 2008) and bio-geographical evaluation (Von et al., 2005). In molluscs, shell shape variation has been reported to distinguish species of similar shape (Innes and Bates, 1999; Aguirre et al., 2006; Rufino et al., 2006; Costa et al., 2008, 2010) or to analyse intra-specific variation along a wide geographical range (Palmer et al., 2004; Krapivka et al., 2007; Marquez et al., 2010).

The winged pearl oyster *Pteria penguin* (Roding, 1798) (family: Pteriidae), is widely distributed in Western Pacific Ocean and Indian Ocean (Southgate et al., 2008). In South China, *P. penguin* is traditionally used for production of half-pearls (‘mabé’). *P. penguin* is considered as an important pearl oyster species in Guangdong, Guangxi and Hainan provinces of China due to its high economic value (Qi et al., 2011). Recently, as consequence of overfishing and habitat deterioration, the natural availability of *P. penguin* has reduced significantly. Moreover, the germplasm resources of *P. penguin* has changed considerably due to the long-term culture of the species without proper...
germplasm management. Therefore, it is necessary to formulate effective germplasm management strategies for *P. penguin*. Recent studies on *P. penguin* focused on aspects like hatchery production (Teitelbaum et al., 2008; Mattew and Southgate., 2012), biofouling (Guenther and De Nys, 2006), polychaete verminosis (Liang et al., 2007), pearl production (Kripa et al., 2008; Kishore et al., 2013), pearl shell lectin (Naganuma et al., 2006), gametogenic process (Arjarasirikoon et al., 2004) and *Pteria* toxins (Takada et al., 2001). Information on the morphological variations in *P. penguin* has not been reported so far. In the present study, 10 morphological characters of *P. penguin* within five established populations from the South China Sea were analysed with the objective of estimating morphometric variability among different populations.

**Materials and methods**

A total 307 samples of *P. penguin* were collected from three wild populations, from Sanya Bay, Beihai Bay and Lingao Bay (designated as Pop. 1, Pop. 2 and Pop. 4 respectively) and two cultured populations (from Xuwen Bay and Li’an designated as Pop. 3 and Pop. 5 respectively) in the South China Sea during October 2013 and June 2014 (Fig. 1, Table 1). All samples were transported live in cool moist condition to the Tropical Fisheries Research and Development Center, South China Sea Fisheries Research Institute, Hainan Province, P. R. China. The samples were scrubbed and washed thoroughly in seawater to remove the fouling organisms and silt, before taking morphometric measurements. Morphometric measurements were taken using a digital vernier caliper (Hangzhou) accurate to 0.01 mm. A total of 5 landmarks and 7 distances were measured (Fig. 2). These landmarks were selected based on the shell structure of *P. penguin*. Further, those landmarks which can be easily observed and assessed by naked eye were selected (Nie et al., 2013). In addition to these, shell length (SL), shell height (SH) and shell width (SW) were also recorded. Linoy Libini et al. (2011) reported that the

![Fig. 1. Map showing the location of study sites (●: sampling sites)](image_url)

**Table 1. Sampling details of *P. penguin* used in the study**

| Populations | Locality | Geographic coordinates | Sample size |
|-------------|----------|------------------------|-------------|
| Pop. 1      | Sanya, Hainan Province, China | 18°25′N,109°39′E | 65 |
| Pop. 2      | Beihai, Guangxi Province, China | 21°07′N,109°11′E | 90 |
| Pop. 3      | Lingao, Hainan Province, China | 20°04′N, 109°63′E | 52 |
| Pop. 4      | Lingshui, Hainan Province, China | 18°43′N, 110°06′E | 50 |
| Pop. 5      | Xuwen, Guangdong Province, China | 20°43′N, 109°94′E | 50 |

Pop. = Population
hinge length in *P. penguin* becomes an unreliable measure, as the posterior ear tips are often broken during collection. Therefore, only samples with undamaged shell, except the posterior ear tips were included and analysed in this study.

Statistical analyses were performed with SPSS 13.0 software (SPSS Inc., Chicago, USA). To remove the effect of size and age, all morphometric characters were standardised according to the equation \( L_s = L/SL \), where \( L_s \) = standardised measurement, \( L \) = measure traits and \( SL \) = shell length of each specimen (Wang et al., 2009).

Descriptive statistics including mean (X), standard deviation (SD) and coefficient of variation (CV = SD/X) of each morphological character within and among populations were calculated using EXCEL 2003 (Microsoft Corporation, Redmond, WA, USA).

Principal component, discriminant factorial and hierarchical cluster analyses were used in this study. Principle component analysis (PCA) was used to reduce the amount of morphometric data and evaluate morphometric variation among specimens and to identify variables responsible for this (Veasey et al., 2001; Samaee et al., 2006, 2009). All PCAs with Eigen value >1 were considered as important (Chatfield and Collins, 1983). Use of the correlation matrix in PCA, in this study, allowed a direct interpretation of character loadings (>0.80) and a direct comparison between populations.

Discriminant function analysis (DFA) was conducted to test the effectiveness of the characters in predicting different group locations, which clarify the relative importance of such traits as discriminators between *a priori* for groups, as performed by Kong et al. (2007) and Konan et al. (2010). A forward stepwise function analysis was carried out to reduce the number of variables (Jain et al., 2000; Poulet et al., 2004; 2005) and to identify the combinations of variables which separate groups (Hair et al., 1996). The classification success rate was evaluated based on the percentage of individuals correctly assigned in to original sample (Silva, 2003; Marques et al., 2006). The relative importance of meristic and morphometric characters in discriminating populations was assessed using the F-to-remove statistic (F-to-enter, 3.84; F-to-remove, 2.71) (Turan et al., 2006). A complement to discriminant analysis i.e., hierarchical cluster analysis (HCA) based on Euclidean nearest neighbour was used to test whether there was any correlation between morphological and geographical distances (Turan et al., 2006; Ferrito et al., 2007).

**Results and discussion**

The present study aimed to assess the morphological variations in different geographic populations of *P. penguin* in South China Sea. The parameters of measured traits are given in Table 2. The coefficients of variation (CVs) of most measured traits from Pop.1 were higher than the other four populations. The highest CVs of D (1-2) was obtained in Pop. 4 (19.82%), while the lowest value (4.18%) was recorded in D (1-3) from Pop. 3. The CVs of all measured traits from five different populations were relatively low (CV<20%, Table 2). Results from the present study showed that intra-population variation in morphometric characters were found to be low for the five geographic populations tested. This was proved by low values of coefficient of variation (CV<20%) for all measured variables and justified that a phenotypically homogeneous group was there within each population (Ferrito et al., 2007; Konan et al., 2010). Recent reports indicated that low values of CV may justify high inheritability (Manuris et al., 1998) and consequently limited influence of environmental variation on morphological variability (Soule and Cuzin-Roudy, 1982). Results of the present study indicated that all the five populations were with low variation and morphologically not much influenced by environmental conditions.

The results of PCA showed that a total of 68% of the total variation associated with the 10 morphometric characters were accounted for the first two principal components in the tested populations, which explain the variability manifested between individuals (Table 3). The characteristics with an Eigen vector of >0.80 were included and the others discarded. PC1 loadings explained 53.84% of the total variations, while only...
14.24% of the total variation was explained by PC 2 (Table 3). PC 1 of the analysis was related to major dimensions of shell outline, including D(1-3)/SL, D(1-4)/SL, D(2-3)/SL, D(2-4)/SL and some traits of shell hinge, such as D(1-5)/SL and D(2-5)/SL. In PC 1, the most important character was D(2-4)/SL, with contribution of 94.1%, D(1-4)/SL followed with the value of 91.5%. Other traits loading on PC 2 was only intensively related to the anterior ear tips and D (1-2)/SL had the maximum contribution (87.1%).

Recent studies have reported that dorso-ventral traits are used as a measure of growth index for *P. penguin* (Linoy Libini et al., 2011; Milione and Southgate, 2011, 2012), which indicated that the major morphological characters for the bivalves reflect both phylogenetic history and life habits (Gordillo et al., 2014). The scores of visual examination of the plots through PC1 and PC2 are presented in Fig. 3. All populations were located in the middle group of the first PC and the second PC

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Table 2. Descriptive statistics of various morphological characters within five populations of *P. penguin*

| Variable | Pop. 1 | Pop. 2 | Pop. 3 | Pop. 4 | Pop. 5 |
|---------|-------|-------|-------|-------|-------|
| SL      | 127.21 ± 14.44 | 120.11±9.56 | 93.26±6.59 | 89.57 ±5.73 | 90.11±5.34 |
| Range   | 82.24 - 162.60 | 91.16-145.5 | 73.52-126.21 | 74.42-104.41 | 74.31-104.46 |
| CV (%)  | 11.35 | 7.96 | 7.07 | 6.40 | 5.92 |
| SH      | 175.04 ± 18.85 | 155.32±12.38 | 114.48±5.94 | 110.16 ±6.81 | 113.05±7.90 |
| Range   | 175.04 - 225.08 | 115.16-190.00 | 97.85-129.11 | 92.39-131.05 | 86.31-162.60 |
| CV (%)  | 10.77 | 5.19 | 5.19 | 6.18 | 6.99 |
| SW      | 54.9 ± 5.79 | 62.09±4.11 | 45.75±2.98 | 49.62 ±3.09 | 46.65±2.77 |
| Range   | 23.37 - 71.23 | 51.32-77.22 | 37.98-51.89 | 36.30-57.34 | 39.43-56.12 |
| CV (%)  | 10.54 | 6.50 | 6.50 | 6.22 | 5.94 |

| Variables | Mean ± SD | Range | CV (%) |
|-----------|-----------|-------|--------|
| SH/SL     | 0.394     | 0.070 |        |
| SW/SL     | 0.480     | 0.604 |        |
| D(1-3)/SL | 0.764*    | 0.060 |        |
| D(1-4)/SL | 0.915*    | -0.178|        |
| D(2-3)/SL | 0.796*    | -0.098|        |
| D(2-4)/SL | 0.941*    | 0.036 |        |
| D(1-2)/SL | 0.151     | 0.871 |        |
| D(1-5)/SL | 0.823*    | -0.327|        |
| D(2-5)/SL | 0.906*    | -0.02 |        |
| Eigen value| 4.845     | 1.282 |        |
| Variance (%)| 53.837    | 14.259|        |
| Cumulative variance (%)| 53.837 | 68.076|        |

Indicates that loading value exceeds 0.75; D (number a - number b): Distance between two landmarks; SL: Shell length; SH: Shell height; SW: Shell width; SD: Standard deviation; CV: Coefficient of variation; Pop.: Population.
The shell shape traits used in the present study have shown to provide an insight into the discrimination of different populations of *P. penguin*.

Discriminant function analysis (DFA) could be a useful method to distinguish different stocks of the same species (Murta et al., 2008). In the present study, the DFA of morphometric characters produced four functions, which explained 100% of the accumulated population variance (Table 4). It was found that 87.9% of the total variance was contributed by the first and second canonical variables (67.80% and 20.10% respectively) indicating that the greatest proportion of the total variance was due to the first two canonical variables (Table 4). The stepwise discriminant analysis retained seven variables that are most discriminant among the different populations (Table 5). These characters of primary importance in distinguishing among the five populations where $D(2-3)$ ($\lambda=0.52$; $F=71.23$; $p<0.001$), $SW$ ($\lambda=0.237$; $F=79.38$; $p<0.001$), $D(1-2)$ ($\lambda=0.179$; $F=60.55$; $p<0.001$), $D(2-5)$ ($\lambda=0.128$; $F=54.90$; $p<0.001$), $D(1-5)$ ($\lambda=0.085$; $F=54.37$; $p<0.001$), $D(2-4)$ ($\lambda=0.070$; $F=49.25$; $p<0.001$) and $SH$ ($\lambda=0.066$; $F=42.81$; $p<0.001$).

Summary statistics indicated that the coefficients $SW/SL$ ($D(1-2)/SL$ and $D(2-5)/SL$) contributed the most to the first 2 discriminant functions, respectively (Table 6). Based on DFA evaluation, the overall random assignment of individuals into their original groups was 81.8% (Table 7), which indicate a high degree of inheritance between populations in shell morphology in the study area. The most well-defined population was found to be Pop.1 with classified individual percentage of 96.90% (Table 7), followed by Pop. 5 (82%) and Pop. 4 (78%). The incorrect percentages in five populations ranged from 2 to 18% and the majority of misclassification proportion (18%) of Pop. 4 has morphometric characters similar to Pop. 5 (Table 7). In addition, only a proportion of 3.1% of Pop.1 was allocated to Pop. 2 and only 4.4% of Pop. 2 was classified as Pop. 1. The confusion matrix ranged from 13.5-18% and the misclassification proportion among Pop. 3, Pop. 4 and Pop. 5 were high. The scatter plots of DFA scores for the study are showed in Fig. 4. Visual examination of the plots of DFA 1 and DFA 2 scores indicated that selected samples are grouped into five major respective areas. This explained the efficiency of discriminator power of morphometric characters used. Indeed, a strong discriminating power of the morphometric variables was found for comparison

![Fig. 3. Scatter plot of principal components from the principal components analysis of different populations of *P. penguin*](image)

### Table 4. Statistical analysis of first three discriminant functions for the ratios of the populations of *P. penguin*

| Function | Value | Variance (%) | Cumulative variance (%) | Chi Square | DF | p   |
|----------|-------|--------------|-------------------------|------------|----|-----|
| 1        | 3.450 | 67.80        | 67.8                    | 813.56     | 28 | <0.001|
| 2        | 1.020 | 20.10        | 87.9                    | 365.66     | 18 | <0.001|
| 3        | 0.497 | 9.80         | 97.7                    | 154.67     | 10 | <0.001|
| 4        | 0.119 | 2.30         | 100                     | 33.60      | 4  | <0.001|

DF: Degrees of freedom; p: Probability value

### Table 5. Discriminatory power of morphometric characters of individuals of *P. penguin* retained by step discriminant analysis

| Variables | Wilk Lambda ($\lambda$) | F to enter/remove | Probability | Tolerance |
|-----------|-------------------------|-------------------|-------------|-----------|
| SH/SL     | 0.070                   | 42.805            | ***         | 0.615     |
| SW/SL     | 0.237                   | 79.384            | ***         | 0.698     |
| D(2-3)/SL | 0.515                   | 71.230            | ***         | 0.371     |
| D(2-4)/SL | 0.070                   | 49.253            | ***         | 0.437     |
| D(1-2)/SL | 0.179                   | 60.546            | ***         | 0.649     |
| D(1-5)/SL | 0.085                   | 54.367            | ***         | 0.528     |
| D(2-5)/SL | 0.128                   | 54.902            | ***         | 0.348     |

*** p<0.001; D (number a - number b): Distance between two landmarks; SL: Shell length; SH: Shell height; SW: Shell width
between populations (Murta, 2000; Garcia-Davila et al., 2005; Ferrito et al., 2007; Anastasiadou and Leonardos, 2008; Anastasiadou et al., 2009). The differences found among the shape of shells could also be explained as the outcome of the phenotypic plasticity of the populations subjected to different environmental conditions (Marquez et al., 2010).

Geographically, Beihai (Pop. 2), Lin’gao (Pop. 4) and Xunwen (Pop. 3) populations were found closer, while a shorter geographical distance was observed between Sanya (Pop. 1) and Lingshui (Pop. 5) (Fig. 1). Hierarchical cluster analysis revealed that the studied populations were clustered into two distinct groups (Fig. 5), demonstrating that there might be considerable morphological divergence among different geographical groups. This result indicated that Xuwen (Pop. 3), Lin’gao (Pop. 4) and Li’an (Pop. 5) populations are geographically close. The results speculated that the source of Li’an culture population might be Xuwen Bay. Sanya (Pop. 1) and Beihai (Pop. 2) populations clustered into one group and the divergent distance between Pop. 1 and Pop. 2 was significantly greater than the other populations (Fig. 5). The discriminant analysis also confirmed above results, which showed that the incorrect percentages between Pop. 1 and Pop. 2 were <5% (Table 7). Recent study showed that the expression of phenotype is largely determined by the environment of the habitat (Brian et al., 2006). But the causes of morphological differences among populations are often quite difficult to be explained (Poulet et al., 2004). Variation in morphometric characters may be affected by genetic and environmental factors (Murta, 2000).

**Table 6. Morphometric variables for P. penguin obtained using Wilk discriminant function**

| Characters | Function 1 | Function 2 | Function 3 | Function 4 |
|-----------|-----------|-----------|-----------|-----------|
| SH        | 1.698     | 0.701     | -4.976    | -0.588    |
| SW        | -17.137   | -7.373    | 13.948    | -3.464    |
| D23       | 7.316     | -0.619    | 3.98      | -4.613    |
| D24       | -2.524    | 3.311     | -8.258    | 10.427    |
| D12       | 8.126     | 15.454    | 14.327    | 10.708    |
| D15       | -3.673    | 8.476     | -0.814    | -1.23     |
| D25       | 0.758     | -14.697   | -0.202    | 1.609     |
| Constant  | -3.203    | 4.57      | -1.246    | -3.131    |

**Table 7. Results of the number of individuals classified and the percent in each group**

| Populations | Predicted group membership |
|-------------|----------------------------|
|             | Pop. 1 | Pop. 2 | Pop. 3 | Pop. 4 | Total |
| Original grouping |       |       |       |       |       |
| Pop. 1      | 63     | 2      | 0      | 0      | 65    |
| Pop. 2      | 4      | 69     | 7      | 5      | 90    |
| Pop. 3      | 0      | 5      | 39     | 1      | 52    |
| Pop. 4      | 0      | 2      | 0      | 39     | 90    |
| Pop. 5      | 0      | 1      | 0      | 8      | 41    |
| Percentage (%) |       |       |       |       |       |
| Pop. 1      | 96.9   | 3.1    | 0      | 0      | 100   |
| Pop. 2      | 4.4    | 76.7   | 7.8    | 5.6    | 100   |
| Pop. 3      | 0      | 9.6    | 75     | 1.9    | 13.5  |
| Pop. 4      | 0      | 4      | 0      | 78     | 18    |
| Pop. 5      | 0      | 2      | 0      | 16     | 82    |

A: 81.8% of original grouped cases correctly classified; Pop. : Population

**Fig. 4. Scatter diagram for discriminant function 1 and discriminant function 2 of P. penguin from five different geographical populations**

**Fig. 5. Dendrogram of P. penguin populations based on morphological characters**

C A S E  0  5  10  15  20  25
Label Number +---------------+-------+-------+------+
| Pop. 3 |                  |
| Pop. 5 |                  |
| Pop. 4 |                  |
| Pop. 1 |                  |
| Pop. 2 |                  |

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Although it is possible to suggest how variations in shell morphology of *P. penguin* could be adaptive in different environments, it is difficult to tease apart the possible explanations due to the complexity of the relationship between phenotype and the local physical and ecological conditions. Further verification of the stock structure may be essential by biological evidence, such as geometric morphometry and genomic analyses.

In this study, the shape analysis proved to be a powerful tool for stock discrimination of *P. penguin* in the South China Sea, representing this species with high probability of interbreeding. The present study demonstrates that five populations of *P. penguin* from different areas of the South China Sea are more or less discriminated on the basis of shape measurements related to D(1-4) and D(2-4). Results from the present study provide valuable information on the population identification of *P. penguin* in the South China Sea which can facilitate the development of management strategies, the design of biological sampling programs and strategies for conserving diversity of this species.

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