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Describing geographic differences in carapace shape in the blue swimming crab *Portunus pelagicus* from Mindanao Bays, Philippines

[1]Maria Lanie S. Sanchez, [1]Jessie G. Gorospe, [1]Jocelyn N. Gorospe, [2]Mark Anthony J. Torres, [2]Cesar G. Demayo

[1] School of Graduate Studies, MSU-Naawan, Naawan, Misamis Oriental, Philippines; [2] Department of Biological Sciences, College of Science and Mathematics, MSU-Iligan Institute of Technology, Iligan City, Philippines. Corresponding author: C. G. Demayo, cgdemayo@gmail.com

Abstract. The shapes of the carapace of populations of the blue swimming crab *Portunus pelagicus* were described using landmark-based geometric morphometrics specifically relative warp (RW) and euclidean distance matrix analysis (EDMA). Results of the study have shown notable carapace shape variation between populations and sexes of *P. pelagicus.* Female *P. pelagicus* have broadened posterior margin of the carapace related to abdomen base while the male have broadened posterolateral region, noticeable anterolateral teeth. While the analysis of covariation of shape and centroid size showed that the carapace shapes of both sexes were size-dependent, dimorphism is argued to be correlated to specific functions carried out by each sex. The observed differences between populations of the species still has to be further elucidated especially regarding the adaptive significance of differences.

Key Words: plasticity, epigenetic, centroid size, euclidean distance.

Introduction. The shape of the carapace in crabs is not only used to describe populations and species (Rathbun 1918; Sullivan 1998; Mallet 2005; Brian et al 2006) but also in ecological (Sardà et al 2005; Giri & Loy 2008) and fishery-related concerns (Cadrin 2000; Chang & Hsu 2004). Generally, the shape in crabs is estimated through curvatures or pairwise comparison of linear measurements (Brian et al 2006). However, allometric changes in morphological shape as shown in many studies (Cheverud 1982; Huber 1985; Klingenberg 2011; Spivak & Schubart 2003; Botello & Alvarez 2006; Costa & Soares-Gomes 2008) indicate that these are important sources of variation and have resulting in many cases of junior synonymy (Santana & Tavares 2010; Osawa & McLaughlin 2010) and misidentification. There is a need therefore to further study shape variations looking for refinements of the analysis like the use of new methods such as landmark-based geometric morphometrics where data for morphometric study usually include geometric locations of landmarks, points that correspond biologically from form to form (Bookstein 1986).

The landmarks link three separate scientific thrusts such as the geometry of data, the mathematics of deformation, and and the biological explanations of the generated shape (Bookstein 1991). It was argued that landmark-based geometric morphometrics is a powerful approach to quantifying biological shape, shape variation, and covariation of shape with other variables or factors (Webster & Sheets 2010).

The geometric morphometric method uses flexible tools of multivariate statistics that make it possible to investigate morphological variation with direct reference to the anatomical context of the structure of a certain species under study (Cavalcanti et al 1999; Ristovska et al 2008; Dorado et al 2012; Moneva et al 2012 a,b,c; Apuan et al 2012; Albutra et al 2012) which in this current study was applied to *Portunus pelagicus* (Linnaeus, 1758), an important crab species in aquaculture in the Philippines. This species is considered a delicacy and commercially important throughout the Indo-Pacific

(BFAR 2009). It has become the fourth top export fisheries product of the Philippines raising revenues of thousands of US Dollars from tons of live/fresh/frozen/chilled crabs, crab meat and crab fats (BFAR 2009). With increasing number of exporters of crab meat based in the country and with most of their produced are going to the USA, only show how important this species to the country's economy. There are concerns however as to the pressures exerted to the crab stocks. Reports in the year 2000 show significant decreased in the CPUE (catch per unit effort) of crabbers (Ingles & Flores 2000) and interviews with many crab collectors say their catch have become scarce. This could be attributed to the fact that the crabs were collected even before they reached maturity including also those that are in their egg-laying stage. Fishery practices such as the use of Danish Seines, push nets, and compressors are also out of control, resulting in catching and landing large volumes of immature individuals and berried female crabs. The Bureau of Fisheries and Aquatic Resources (BFAR) are now on the process of adopting the Blue Swimming Crab (BSC) Management Plan to avert a possible catastrophe in crab fishery by implementing a sustainable fishery project. Since the species is fast-growing with ease of larviculture, high fecundity and relatively high tolerance to both ammonia (Romano & Zeng 2007a) and nitrate (Romano and Zeng 2007 b, c) makes this species ideal for aquaculture. It was therefore necessary a survey of the stock sources of this species, understanding its ecology and biology be done. Since Mindanao Island is not yet exploited, it is now considered to be a good source of the species for export thus it was necessary that the populations of this species be investigated.

Material and Method

Study area. *P. pelagicus* samples were obtained directly from the crab collectors of selected areas in Mindanao.

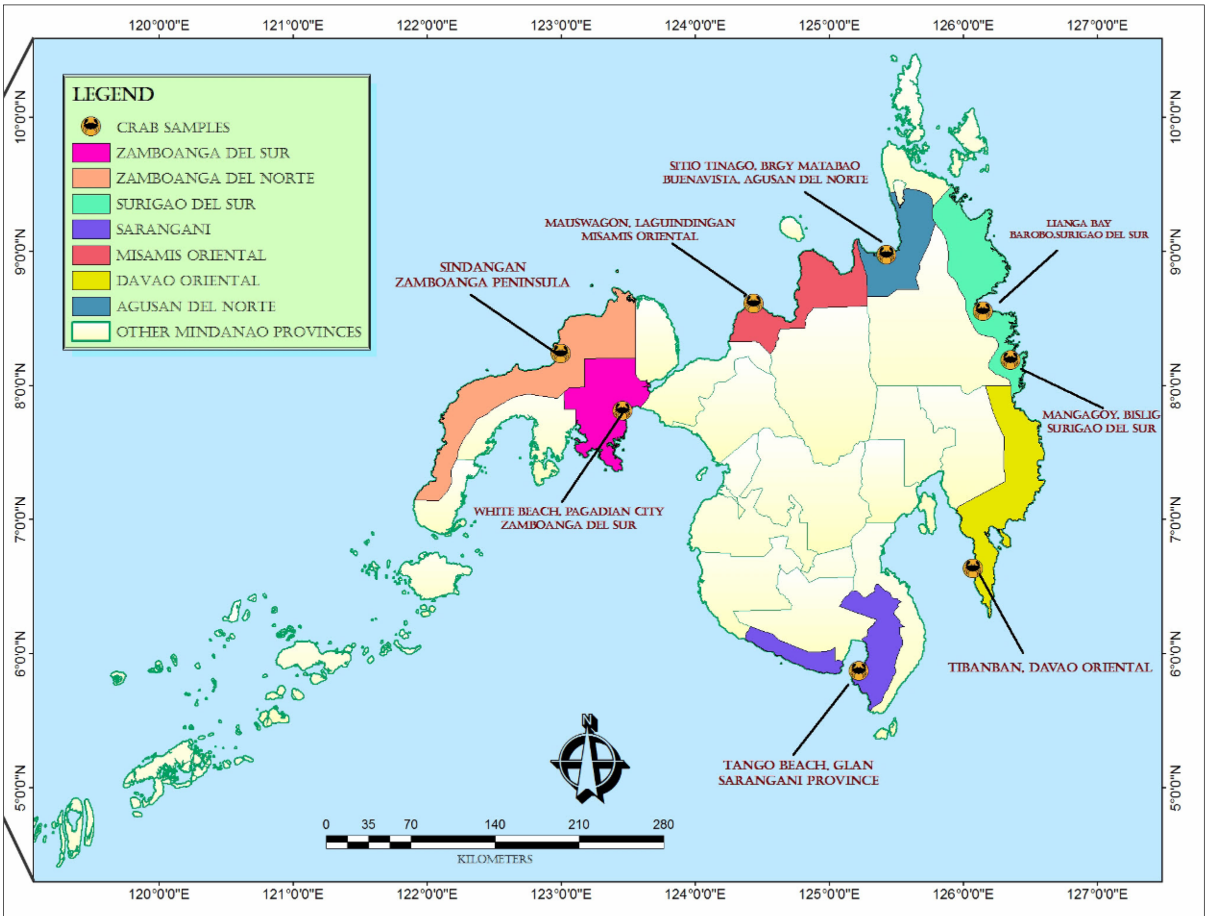

Figure 1. Collection of *P. pelagicus* in Mindanao. The crabs were collected from the bay areas by commissioned crab fishermen (Map modified from Google.com).

In the Davao gulf area, crabs were collected in Tibanban, Governor Genoroso, Davao Oriental (6°38'4.81"N, 126° 4'19.21"E), in Lianga Bay, collections were in Barobo, Surigao del Sur (8°33'21.90"N, 126° 8'45.03"E) and in Bislig Bay at Mangagoy, Bislig, Surigao del Sur (8°11'22.19"N, 126°21'5.14"E), in Butuan Bay at Sitio Tinago, Barangay Matabao, Buenavista, Agusan del Norte, in Macalajar Bay at Mauswagon, Laguindingan, Misamis Oriental (8°36'46.85"N, 124°25'55.46"E), in Iliana Bay at "White beach", Pagadian City, Zamboanga del Sur (7°48'50.52"N, 123°27'19.76"E), in Sindangan Bay at Sindangan, Zamboanga del Norte (8°14'18.27"N, 122°59'43.92"E) and in Sarangani Bay at Tango Beach located at the Southern portion of the municipality of Glan (5°52'16.31"N, 125°13'14.41"E) (Figure 1).

Sample preparation for imaging. Collection of the *P. pelagicus* in selected areas of Mindanao Bays was done once per area from 4 to 13 May 2012 with at least 80 adults from each area. Collected samples were immediately sexed based on external morphology such as its abdomen, size and color, weighed (to the nearest gram) using a Dahongying ACS-30 digital weighing scale. The carapace was then dissected for scanning purposes. To analyse the carapace shape in *P. pelagicus*, each carapace was scanned in tri-replicates using an Hp G2410 Flatbed Scanner at an optical scanning resolution of 1200 dpi.

Landmarks selection. Fifty-two (52) landmarks (equivalent to 52 X and 52 Y Cartesian coordinates) covered the whole carapace area were selected to provide a comprehensive summary of the shape variation and symmetry of the carapace (Zelditch et al 2004) (Figure 2). The descriptions of the landmarks are presented in Table 1. The two-dimensional Cartesian coordinates of 52 landmarks were digitized by tpsDig ver.1.39 software (Rohlf 2004). Measurement error was reduced by digitizing the carapace in tri-replicates (Dvorak et al 2005). The tps digitizer software obtain the x and y coordinates of the 52 landmark points which are the raw data used for further analysis. The landmark configurations obtained were then scaled, translated, and rotated against the consensus configuration by GLS (General Least Squares) Procrustes superimposition method (Bookstein 1991; Rohlf & Marcus 1993; Dryden & Mardia 1998).

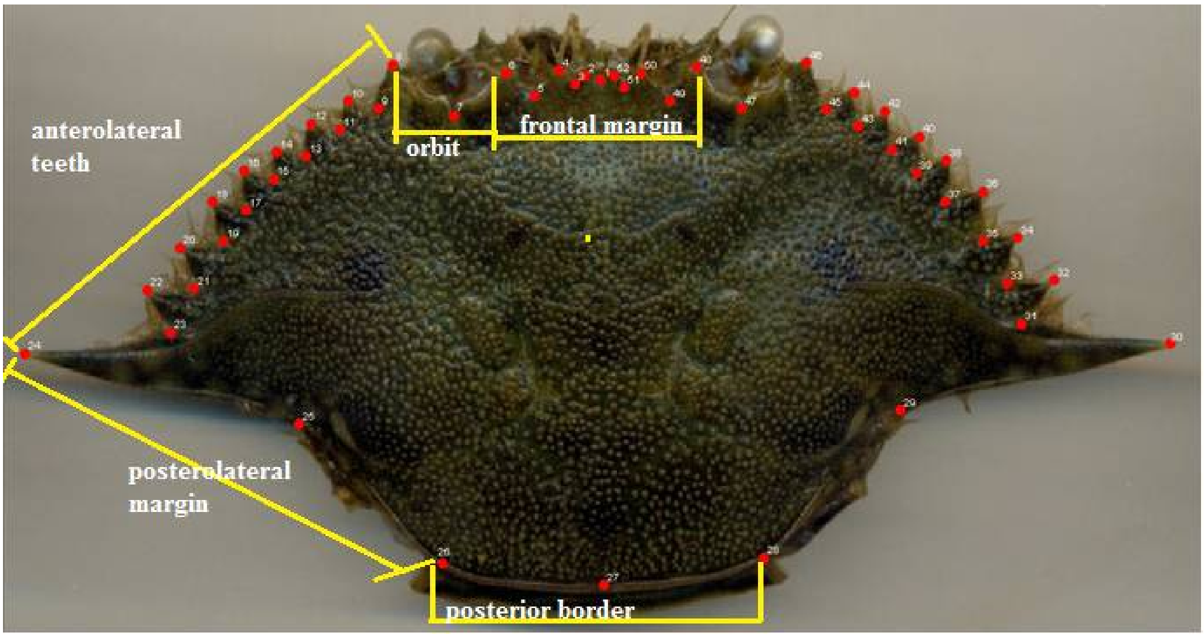

Figure 2. The fifty-two landmarks in the carapace in *P. pelagicus*.

Table 1

Anatomical landmarks of the carapace of *P. pelagicus*

Landmark	*Description of landmark*
1	Center of the frontal margin
2-5	Frontal margin
6-7	Orbital region (left)
8	1st antero-lateral tooth (left)
9	In between 1st and 2nd antero-lateral tooth (left)
10	2nd antero-lateral tooth (left)
11	In between 2nd and 3rd antero-lateral tooth (left)
12	3rd antero-lateral tooth (left)
13	In between 3rd and 4th antero-lateral tooth (left)
14	4th antero-lateral tooth (left)
15	In between 4th and 5th antero-lateral tooth (left)
16	5th antero-lateral tooth (left)
17	In between 5th and 6th antero-lateral tooth (left)
18	6th antero-lateral tooth (Left)
19	In between 6th and 7th antero-lateral tooth (Left)
20	7th antero-lateral tooth (left)
21	In between 7th and 8th antero-lateral tooth (left)
22	8th antero-lateral tooth (left)
23	In between 8th and 9th antero-lateral tooth (left)
24	9th antero-lateral tooth (left)
25	Posterolateral region (left)
26	Posterior base of the abdomen (left)
27	Posterior margin of the carapace
28	Posterior base of the abdomen (right)
29	Posterolateral region (right)
30	9th antero-lateral tooth (right)
31	In between 8th and 9th antero-lateral tooth (right)
32	8th antero-lateral tooth (Right)
33	In between 7th and 8th antero-lateral tooth (right)
34	7th antero-lateral tooth (right)
35	In between 6th and 7th antero-lateral tooth (right)
36	6th antero-lateral tooth (right)
37	In between 5th and 6th antero-lateral tooth (right)
38	5th antero-lateral tooth (right)
39	In between 4th and 5th antero-lateral tooth (right)
40	4th antero-lateral tooth (right)
41	In between 3rd and 4th antero-lateral tooth (right)
42	3rd antero-lateral tooth (right)
43	In between 2nd and 3rd antero-lateral tooth (right)
44	2nd antero-lateral tooth (right)
45	In between 1st and 2nd antero-lateral tooth (right)
46	1st antero-lateral tooth (right)
47-48	Orbital region (right)
49-52	Frontal margin

Relative warps analysis. The relative warps analysis (Bookstein 1991) was performed using the tpsRelw version 1.46 (Rohlf 2008). This analysis corresponds to a principal components analysis (PCA) of the covariance matrix of the partial warp scores, which are different scales of a thin-plate spline transformation of landmarks. According to Hammer et al (2001), usually the most informative are the first and second relative warps. Thin-plate splines was used in order to graphically illustrate patterns of shape variations based on the landmarks which represents the transformation of the reference to each specimen (Bookstein 1991). From the reference configuration, the principal warps were calculated to define a set of coordinate axes for tangent space approximating the curved shape space to which the shapes of specimens can be compared using standard linear statistical methods. The x- and y-coordinates of the aligned specimens onto the principal warp axes are then projected.

The raw coordinate data was also subjected to Euclidean Distance Matrix Analysis (EDMA) to measure all possible chords between landmarks just as if a caliper has recorded these distances earlier. The form matrix does not change and transforms landmark data into a data matrix with a set of consisting distances between all pair of landmarks (Hammer et al 2001) (Figure 3).

Population datasets were pooled and was analyzed using canonical variate analysis to determine variation among populations as expressed relative to the pooled within-group variation. CVA was used in order to compare patterns of interpopulation variation. As a form of multivariate measure, the Wilk's lambda would determine the relationship between several variables. The analysis made use of the Palaeontological Statistics (PAST) software (Hammer et al 2001).

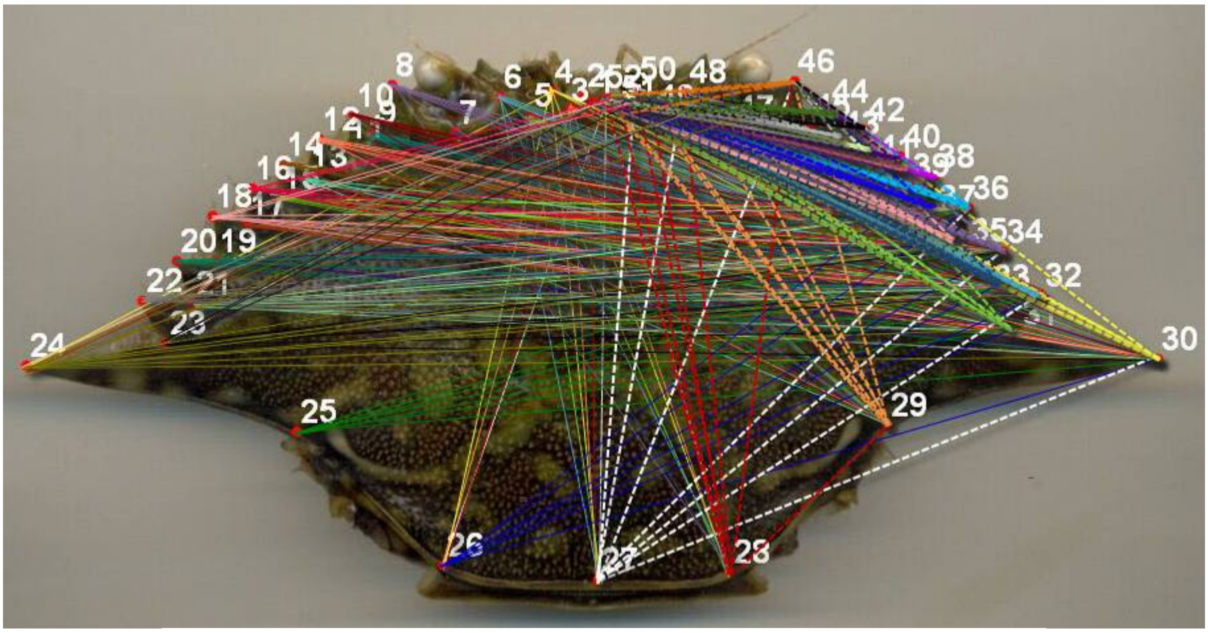

Figure 3. Interlandmark distances in the carapace of *P. pelagicus*.

Results and Discussion. Using the fifty-two landmarks for the carapace, the CVA scatterplots revealed significant variations among geographically different populations of *P. pelagicus* (Figure 4). Significant differences in carapace shapes can be seen based on the distribution of the samples along the first two canonical variate axes among female populations (Wilks lambda = 0.07749; P-value = 0.00) and for the males (Wilks lambda = 0.1862; P-value = 3.874E-318).

Intrapopulational differences in body shapes between sexes were summarized in Table 2. The descriptions of shape variations in the carapace were based on deviations from the consensus shape (Figure 5). The non-affine or non-uniform carapace shape changes were expressed as deformations and shape differences are expressed as bending energy matrix which quantifies the amount and the spatial distribution of 'energy' required to achieve any anisotropic deformation of the reference landmark configuration. The components with large bending energies describe small-scale deformations, whereas small bending energies indicate large-scale deformations. Comparing between female and male carapaces, it was observed that the female carapace have large-scale deformations compared to male carapace in Bislig, Buenavista, Laguindingan, and Sindangan. The opposite was observed for male carapace in Glan, Lianga, Pagadian, and Tibanban (Figure 5). These deformations were described as shown by the relative warps are presented in Table 2. It can be seen that the variations between sexes within a population can be observed in the anterolateral teeth, posterolateral regions and posterior margin of the carapace.

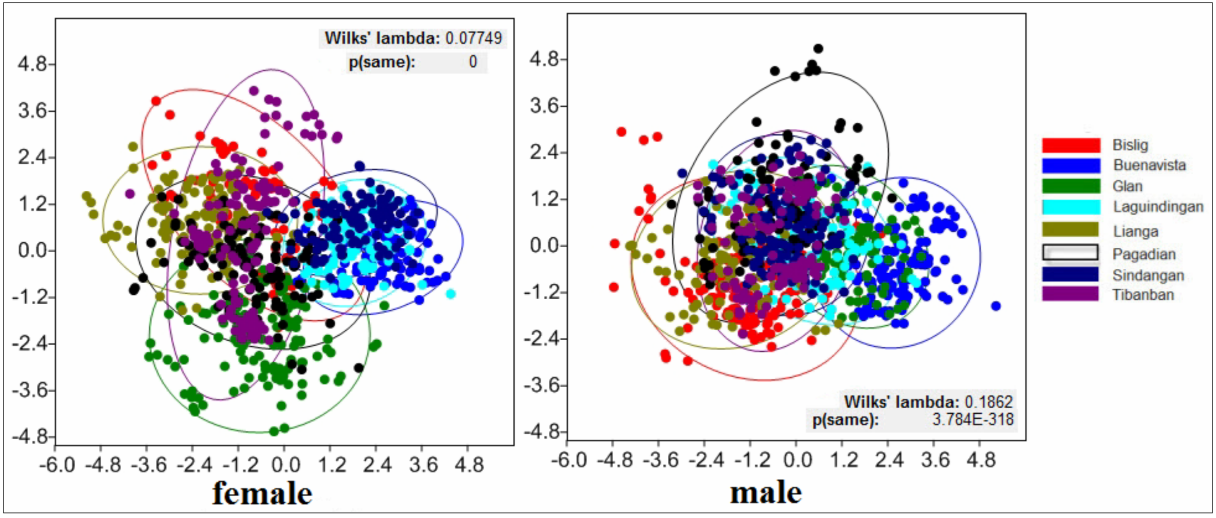

Figure 4. Distribution of the eight populations of the two sexes of *P. pelagicus* along the first two canonical variate axes (a-female, b-male).

Table 2

Variations observed in the carapace shape of female and male *P. pelagicus*

Study area	*Female*	*Male*
Bislig	Variation in the posterior margin of the carapace and 9th anterolateral tooth. RW = 58.82 %	Variation in the 9th anterolateral tooth. RW = 63.08 %
Buenavista	Variation in the anterolateral teeth but more apparent at the right side. RW = 68.38 %	Variation in the posterolateral region RW = 73.34 %
Glan	Variation in the 9th anterolateral teeth and posterior margin of the carapace. RW = 69.41 %	Variation in the anterolateral teeth with different directions on both sides. RW = 69.63
Laguindingan	Variation in the left 9th anterolateral tooth. RW = 76.26 %	Variation in the anterolateral teeth but more apparent at the right side. RW = 65.63 %
Lianga	Variation in the anterolateral teeth but more apparent at the right side. RW = 62.76 %	Variation in the 9th anterolateral teeth and posterolateral region of the carapace. RW = 71.19 %
Pagadian	Variation in the anterolateral teeth but more apparent at the right side; variation in the posterior margin of the carapace. RW = 60.63 %	Variation in the anterolateral teeth. RW = 65.05 %
Sindangan	Variation in the anterolateral teeth. RW = 64.86 %	Variation in the right 9th anterolateral tooth; variation in the posterolateral region of the carapace. RW = 65.59 %
Tibanban	Variation in the right 9th anterolateral teeth. RW = 69.81 %	Variation in the anterolateral teeth with different directions on both sides, posterolateral region, and posterior margin of the carapace. RW = 66.67 %

The shape of the carapace in the two sexes of *P. pelagicus* was further described by determining the landmarks that have contributed to the variations based on the results of the principal component analysis of the RW scores (Table 3). Based on the highest PCA loading value for both sexes, sources of the variations were attributed to deformations in landmark 24 or the left 9th anterolateral teeth and in landmark 23 situated between 9th

and 8th anterolateral teeth. For the female carapace, most of the sources of variations in the female carapace were associated with deformations in the x coordinates of landmarks 20 to 24 (left anterior part), Y coordinates of landmark 26 (left posterior part) and 27 (posterior margin), and deformations in landmarks 30, 31, 32, 34, and 35 (right anterior part). On the other hand, most of the highest PCA loading values for male carapace were represented by deformations in the x coordinates of landmarks 20 to 24 (left anterior part), Y coordinates 25 to 26 (left posterior part), 27 (posterior margin), 28 (right posterior part) and X coordinates of landmarks 30 to 34 (right anterior part) (Table 4).

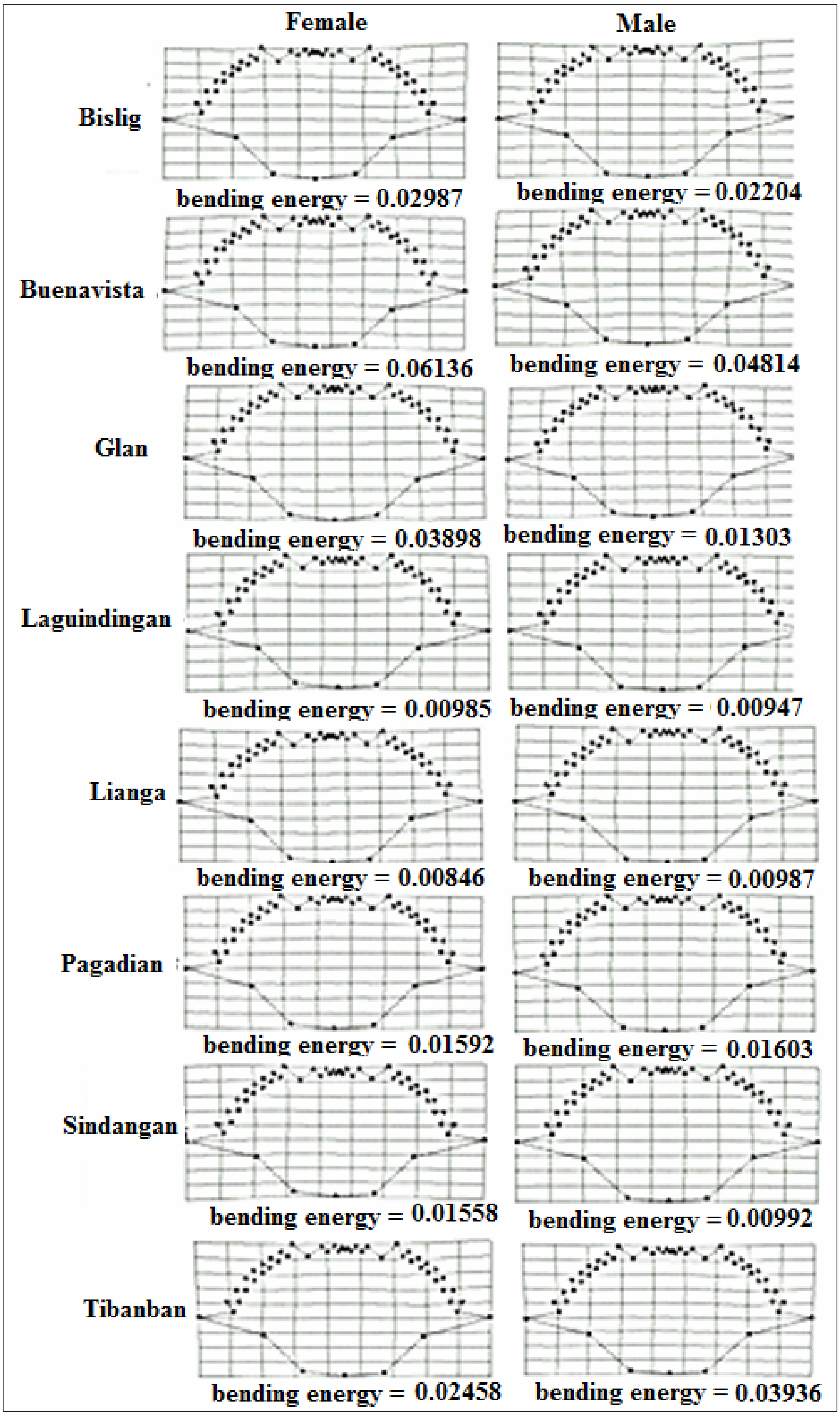

Figure 5. Thin-plate Spline Transformation grid showing the consensus morphology of the carapace of eight populations of the male and female *P. pelagicus* (bending energy at the bottom of the figure).

Table 3

Proportion of variation of carapace with the significant components of *P. pelagicus*

PC	Female		Male	
	Eigenvalue	*% Variance*	*Eigenvalue*	*% Variance*
1	283256	86.059	219321	83.794
2	36812.5	11.184	33314.8	12.728
3	7512.72	2.2825	7729.94	2.9533

Table 4

Variable with the highest PCA loading values for the significant components of the landmark coordinates of the carapace

Principal component	*Female*		*Male*	
	Variables	*Values*	*Variables*	*Values*
1	X30	0.1742	X30	0.185
	X31	0.161	X32	0.1652
	X32	0.1609	X31	0.1622
	X34	0.1557	X34	0.1588
	X35	0.1503	X33	0.158
2	X30	-0.1519	X30	-0.1483
	Y27	0.1412	Y27	0.1406
	X32	-0.1383	Y26	0.1393
	Y26	0.1369	Y28	0.1374
	X31	-0.1363	Y25	0.1272
3	X24	0.2453	X24	0.2683
	X23	0.2272	X22	0.2321
	X22	0.2268	X23	0.2269
	X20	0.2194	X21	0.2177
	X21	0.2186	X20	0.2173

Table 5 shows only one component contributes to carapace variation in *P. pelagicus* based on interlandmark distances. This component accounts for the variance in the multidimentional data according to the Euclidean distance matrix. Table 6 shows the top fifteen interlandmark distances that contribute to the carapace variation in eight populations of *P. pelagicus* (Figure 6).

To be able to understand whether the variations observed were size correlated, covariating centroid size and shape of the carapace was done and the results are presented in Figures 7 and 8. It can be seen from the results that variation in the carapace shapes among populations for female and male *P. pelagicus* were generally size-dependent (female r value = 0.75237; male r value = 0.65999). The xy-plot for female and male carapace representing different size classes, show Tibanban population was discontinuous and for other populations like in Lianga and Sindangan population was found to be continuous.

Table 5

EDMA proportion of variation associated with most significant components of the carapace

PC	Female		Male	
	Eigenvalue	*% Variance*	*Eigenvalue*	*% Variance*
1	2535330	99.41	1713770	97.895
2	6672.62	0.26163	20686.9	1.1817
3	4007.14	0.15712	9015.66	0.515

Table 6

The interlandmark distances with the highest PCA loading values for the significant component of the landmark coordinates of the carapace

Principal component	*Female*		*Male*	
	Interlandmark distances	*Values*	*Interlandmark distances*	*Values*
1	24-30	0.06138	24-30	0.08301
	24-31	0.05759	24-32	0.06836
	22-30	0.05737	22-30	0.06769
	24-32	0.05733	23-30	0.06747
	23-30	0.05709	24-31	0.06726
	24-33	0.05598	24-34	0.06599
	24-34	0.05581	24-33	0.06553
	20-30	0.05563	21-30	0.06527
	21-30	0.05561	20-30	0.06503
	19-30	0.05401	24-36	0.0640
	24-35	0.05388	24-35	0.06384
	18-30	0.05385	18-30	0.06337
	24-36	0.05371	19-30	0.06319
	22-31	0.05352	24-38	0.06193
	23-31	0.05329	24-37	0.06185

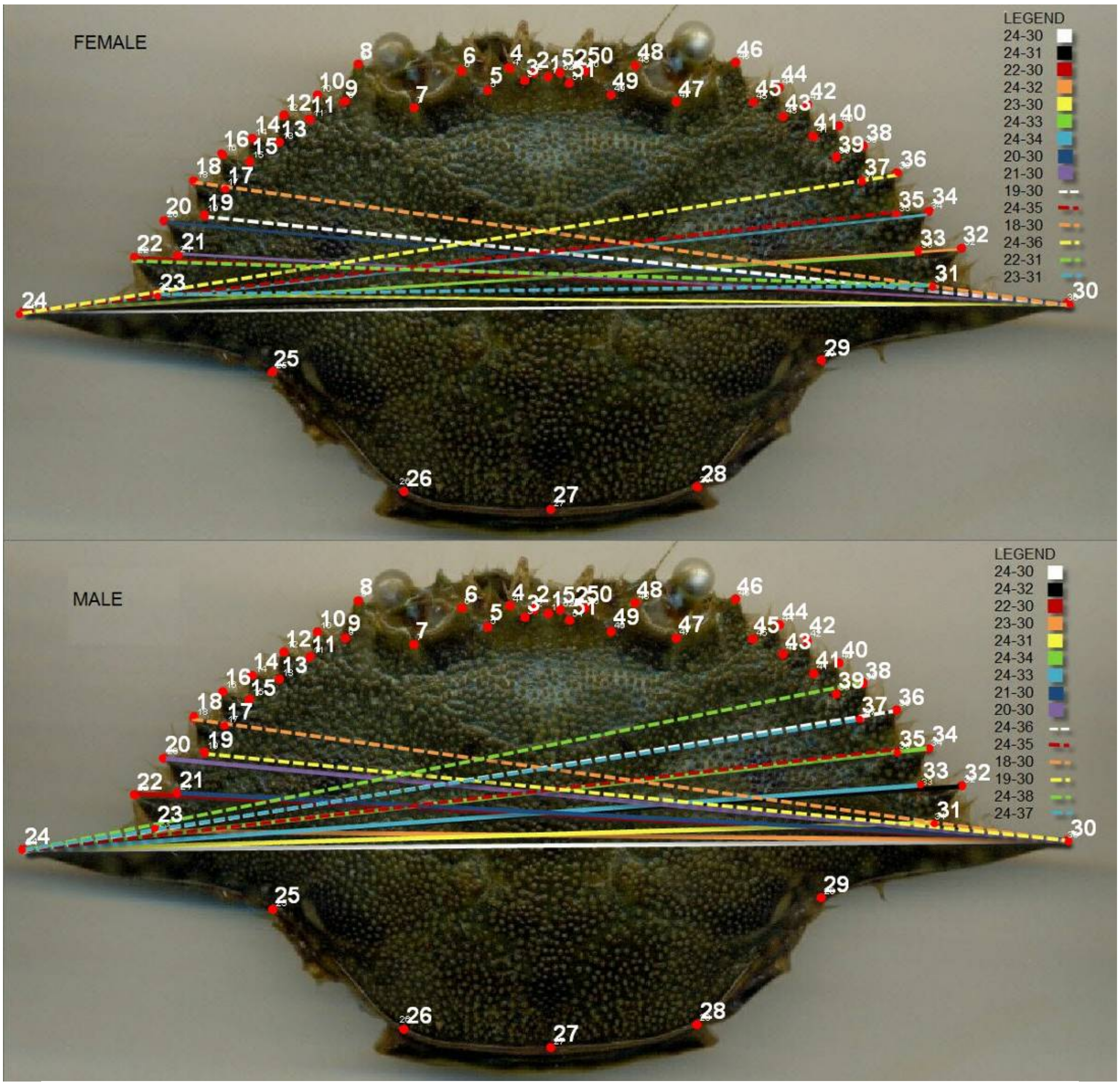

Figure 6. The interlandmark distances with the highest PCA loading values for the significant components of the landmark coordinates of the carapace.

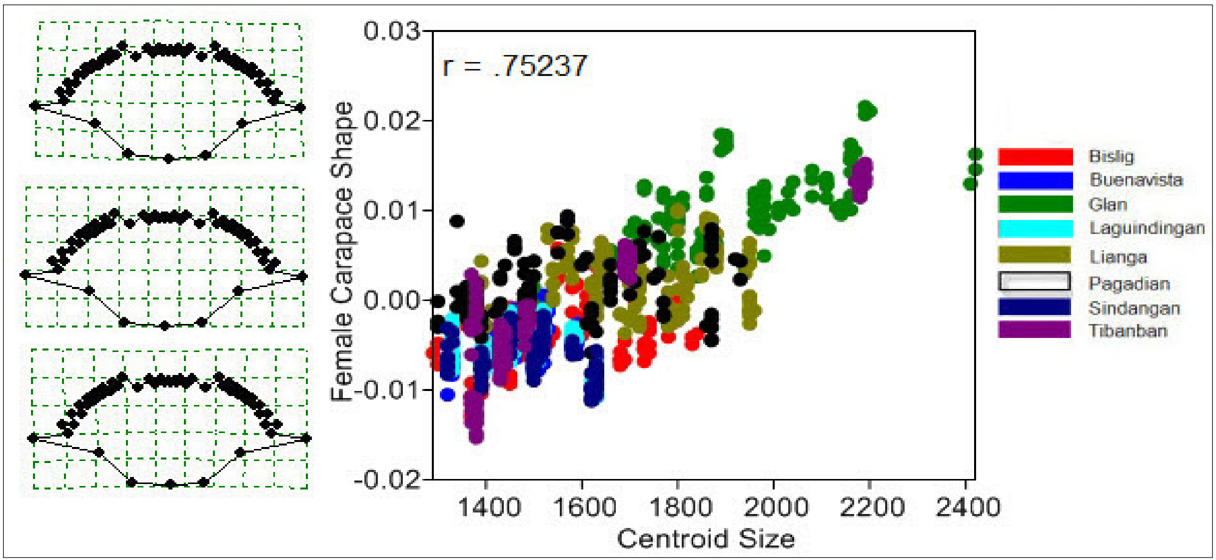

Figure 7. Relationship between shape and size of female carapace of the different populations of *P. pelagicus*.

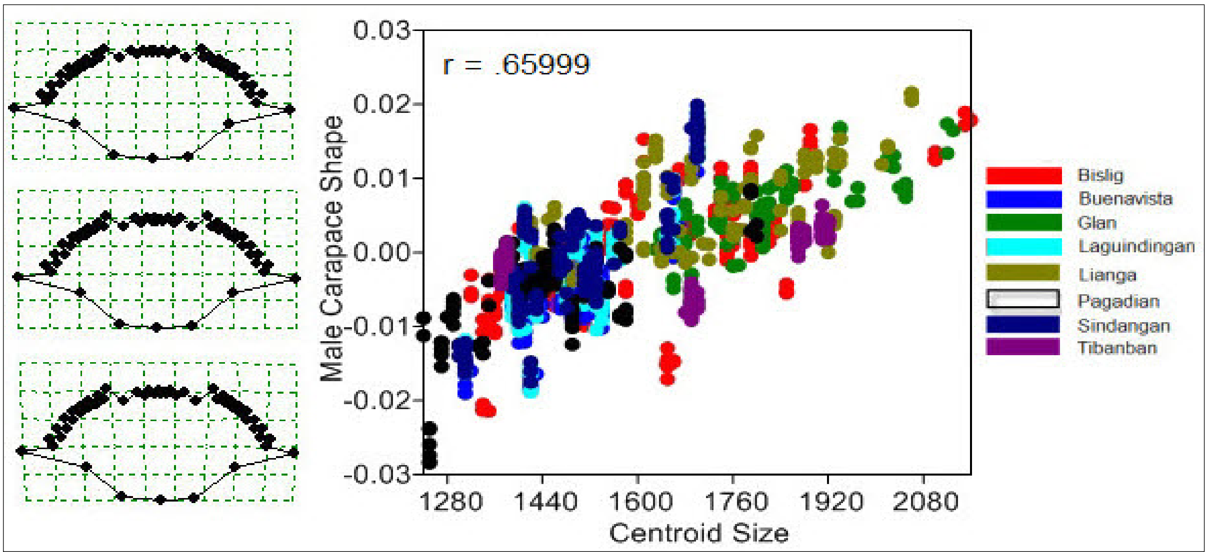

Figure 8. Relationship between shape and size of male carapace of the different populations of *P. pelagicus*.

It can be seen from the results of the study that there is a notable carapace shape variation between sexes and among populations of *P. pelagicus.* Differences among populations based on RW and EDMA showed differences in carapace in both sexes suggesting that sexual dimorphism is evident in *P. pelagicus.* Sexual dimorphism can serve as an initial assessment of the strength of sexual selection and may help to identify characters likely to be the subject of selection (Berkunsky et al 2009). Female *P. pelagicus* have broadened posterior margin of the carapace which is related to abdomen base for greater relative volume for gonad development and external surface for carrying eggs on the abdominal pleopods (Rufino et al 2004). Male *P. pelagicus* have broadened posterolateral region, noticeable anterolateral teeth, which is essential for fighting, defense, or agonistic encounters within and between sexes.

Analysis of covariation of shape and centroid size showed that female and male carapace shapes were size-dependent indicating that the carapace shape may have been due to ontogenetic allometry, age at maturity, nourishment, ecological conditions of the water body (Garth 1957; Hines 1989; Mashiko 2000; Arshad et al 2006; Orensanz et al 2007), predation pressure and food availability (Hines 1989). This may also explain the results of variations observed among populations of the crabs collected from different bays. The variations can also be due to phenotypic plasticity brought about by differences in maximum body size (Hopkins & Thurman 2010), differences in reproductive patterns, growth rates and mortality and differences in environmental conditions (Orensanz et al 1991; Cadrin 2000) as commonly observed with many crab species (Rosenberg 2002; Rufino et al 2004) and in other decapods species (Giri & Loy 2008; Barría et al 2011). It may also be that specialized phenotypes adapted to local environmental conditions (Kingsolver et al 2002) were developed in *P. pelagicus* though it is still difficult to provide a link between the carapace shape and environmental/epigenetic factors (Giri & Loy 2008; Barría et al 2011) as this is still poorly understood and not done in this current study.

Conclusion. In this study, sexual dimorphism in carapace shape was observed in *P. pelagicus* as shown by relative warp and euclidean distance matrix analysis. While it can be argued that dimorphism in carapace shape is related to specific functions carried out by each sex, differences between populations of the species still have to be further elucidated. More studies on the geometric morphometrics of the carapace shape should be coupled with functional hypotheses regarding the adaptive significance of differences.

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Authors:
Maria Lanie S. Sanchez, School of Graduate Studies, MSU-Naawan Campus, Naawan, Misamis Oriental, Philippines, e-mail: glanie89@yahoo.com
Jessie G. Gorospe, School of Graduate Studies, MSU-Naawan Campus, Naawan, Misamis Oriental, Philippines, e-mail: jingorospe@gmail.com
Jocelyn N. Gorospe, School of Graduate Studies, MSU-Naawan Campus, Naawan, Misamis Oriental, Philippines, e-mail: joyce.gorospe@gmail.com
Mark Anthony J. Torres, Department of Biological Sciences, College of Science and Mathematics, MSU-Iligan Institute of Technology, Iligan City, Philippines, e-mail: Torres.markanthony@gmail.com
Cesar G. Demayo, Department of Biological Sciences, College of Science and Mathematics, MSU-Iligan Institute of Technology, Iligan City, Philippines, e-mail: cgdemayo@gmail.com.

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