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Morphological discrimination of populations of the sword shrimp, *Mierspenaeopsis hardwickii*, along Peninsular Malaysian waters by traditional and truss-network approaches

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Abstract. Traditional morphometric approaches have long been used to describe organisms and detect shape variations both within and among groups. However, advanced techniques such as truss-network systems offer better visualisation of shape variation. The data obtained from these approaches are essential for comprehensive stock assessments and play a significant role in developing effective fisheries management strategies. This study compares the efficiency of two morphometric methods (traditional vs. truss-network) in detecting morphological differences between populations of the commercially important sword shrimp, *Mierspenaeopsis hardwickii* (Miers, 1878) in the coastal waters of Peninsular Malaysia. A total of 88 *M. hardwickii* individuals from seven localities in the South China Sea and the Strait of Malacca were analysed using both approaches. Additionally, a discriminant analysis (DA) using Canonical Variate Analysis (CVA) was conducted to classify each population correctly, and an exploratory Principal Component Analysis (PCA) was conducted to quantify and visualise population differences. The results showed that truss-network morphometrics outperformed traditional methods in discriminating among *M. hardwickii* populations. The scatterplots of the first two PC scores, and wireframe analysis demonstrated significant shape differences, suggesting that the populations constitute specific-stock units for fisheries management. This finding implies ecological or life-history adaptations among *M. hardwickii* populations. Incorporating truss-network morphometric data into *M. hardwickii* stock assessments could contribute to a better understanding of population structure and dynamics to support sustainable fisheries management.

Key words. traditional morphometrics, truss-network, shape variation, sword shrimp, stock assessment, Crustacea, Decapoda, Penaeidae

INTRODUCTION

Morphometric studies are widely used to examine shape variation and to analyse its covariance with other variables (Norman, 2017). According to Cadrin (2000), morphological studies of decapod crustaceans have been extensively applied for various purposes, including the development of effective management strategies for conserving threatened species and the identification and differentiation of fishery stocks. Additionally, this approach enables researchers to integrate these quantitative descriptions into statistical analyses, facilitating better interpretation of the collected data. Since the 1980s, various morphometric techniques have been employed to discriminate within and between populations, including traditional morphometrics, truss-network systems, and geometric morphometrics (Cadrin, 2000; Klingenberg, 2011; Adam et al., 2013; Fernando & Amarasinghe, 2014; Tripathy, 2020; Andreella et al., 2023).

Traditional morphometric measurements, also known as linear distance measurements, have long been used to describe patterns of shape variation within and among groups (Norman, 2017). This approach is straightforward and often includes counts, ratios, areas, and angle measurements. Traditional morphometric methods have played a key role in past studies, particularly in research on penaeid shrimps (Cadrin, 2000; Melo & Masunari, 2017). With the advancements in morphometric techniques (Adams et al., 2004; Adams et al., 2013), landmark-based approaches such as truss-network and geometric morphometrics have emerged. These advanced methods provide powerful analytical and graphical tools for quantifying and visualising morphological variation within and among populations, as demonstrated in recent studies on penaeid and palaemonid shrimps (Moraes et al., 2021; Nogueira et al., 2023; Miazaki et al., 2024). These

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developments have significantly improved the precision and depth of morphological studies.

Research on shrimp morphology and the characterisation of morphotypes, both within and among populations, dates back to the early 20th century. Previously, traditional studies on crustacean morphology emphasised allometric relationships to distinguish between species or identify growth patterns (Wardiatno & Tamaki, 2001; Pramithasari et al., 2017). In recent decades, however, advanced morphometric measurements such as truss-network and geometric morphometrics, have emerged as more refined tools, capable of detecting subtle shape differences and improving taxonomic resolution. For example, Moraes et al. (2021) successfully applied geometric morphometrics to differentiate native and non-native species of *Litopenaeus* Pérez Farfante, 1969 along the East Atlantic, highlighting its effectiveness in species discrimination. Similarly, Miazaki et al. (2024) leveraged advanced morphometric measurements to explore sexual dimorphism in shrimps in the genus *Xiphopenaeus* Smith, 1869, contributing novel insights into female morphological discrimination. Additionally, Melo & Masunari (2017) highlighted that the rigid exoskeleton of crustaceans allows for precise biometric measurements, facilitating the detection of subtle morphological changes that are often missed by conventional morphometric methods. This finding highlights the value of advanced morphometric techniques in understanding shrimp population dynamics and structure.

The sword shrimp, *Mierspenaeopsis hardwickii* (Miers, 1878), is a commercially important species within the family Penaeidae Rafinesque, 1815. It is widely distributed across the Indo-West Pacific region, from Pakistan to Taiwan and Indonesia (Chan, 1998; Hurzaid et al., 2020). Within Malaysia, it is found in both the Strait of Malacca (SOM) and the South China Sea (SCS), including the waters off Sabah and Sarawak, with the highest abundance recorded in Peninsular Malaysia (Chan, 1998). This species has become an important crustacean resource in Malaysian fisheries due to its economic value as an affordable protein source and its contribution to national economic growth (Hurzaid et al., 2023). However, many marine shrimp populations are declining globally due to overexploitation and inadequate fisheries management (Hurzaid et al., 2023). Therefore, understanding the morphometric variations of *M. hardwickii* across different populations is crucial for effective conservation and sustainable fisheries management. Morphometric analysis provides a basis for assessing stock structure and can be applied in short-term studies and in examining environmentally induced variation, ultimately supporting sustainable fisheries management (Murta, 2000; Pinheiro et al., 2005).

This study compares the effectiveness of two morphometric measurement methods (traditional morphometrics vs. truss-network analysis) in quantifying and describing morphological differences among *M. hardwickii* populations along Peninsular Malaysia's coastal waters. The aim is to evaluate the potential of these approaches in discriminating among populations by evaluating their classification accuracy using discriminant analysis (DA).

MATERIAL AND METHODS

Sample collection, species identification, and sample storage. A total of 88 specimens of *Mierspenaeopsis hardwickii* were collected from the coastal waters of Peninsular Malaysia between February 2022 and December 2022. Sampling was conducted at seven sites: three along the Strait of Malacca on the west coast namely Kuala Perlis (PRL), Kuala Selangor (SEL), and Batu Pahat (BP); and four along the South China Sea on the east coast namely Endau (END), Kuala Besut (BST), Kuantan (KUN), and Kuala Besar (KB). The different populations were named according to their respective collection sites (Fig. 1, Table 1). Species identification was initially performed using morphological keys provided by Pérez-Farfante & Kensley (1997), and Chan (1998), and further validated through DNA sequence analysis of the mitochondrial cytochrome oxidase subunit I (COI) gene (Hurzaid et al., 2020; Halim et al., 2022).

All species of the genus *Mierspenaeopsis,* including *M. hardwickii*, exhibit male rostral polymorphism (Hsu & Chan, 2023). Typically, *M. hardwickii* has a long, sigmoidal rostrum that extends well beyond the antennular peduncle, the distal third or half of which is without dorsal teeth (Hsu & Chan, 2023). To minimise potential biases associated with seasonal variation during sample collection, only adult female specimens from all *M. hardwickii* populations were used in this study, with population sizes ranging from 10 to 16 individuals per locality. To ensure consistency, only adult female specimens measuring ≥ 6 cm in body length (excluding the rostrum) were selected in the analysis. The determination of the adult female status was based on gonadal maturation and detailed morphological covariates, which provided more accurate and biologically meaningful indicators of reproductive maturity. In female penaeid shrimps, the thelycum (a hardened external reproductive structure) develops progressively as individuals approach sexual maturity and becomes more prominent in fully mature individuals (Chan, 1998). Rahimah et al. (2024) reported a significant correlation between overall body growth (including body length) and reproductive development. Additionally, the typical adult size for both male and female *M. hardwickii* ranges from 6 cm to 10 cm (Chan, 1998). Each specimen was photographed using a Nikon DSLR D5100 equipped with a YONGNUO YN 50 mm F1.8N lens. All images were captured manually, with the distance between the lens and the specimen standardised at approximately 40 cm. Specimens were properly preserved in 95% ethanol and subsequently deposited in the invertebrate collections at the Zoological Reference Laboratory, Universiti Sains Malaysia, Penang. The voucher specimen numbers are as follows: Kuala Perlis (USM_INV001–USM_INV010), Kuala Selangor (USM_INV094–USM_INV108), Batu Pahat (USM_INV274–USM_INV286), Endau (USM_INV353–

Table 1. Sampling locations and corresponding sample sizes of *M. hardwickii* populations collected in this study.

Location	Abbreviation	Water body	Coordinates	Sample size (n)
Kuala Perlis, Perlis	PRL	Strait of Malacca	6°24′00″ N, 100°07’49” E	10
Kuala Selangor, Selangor	SEL	Strait of Malacca	3°20′33″ N, 101°15′13″ E	14
Batu Pahat, Johor	BP	Strait of Malacca	1°40′39″ N, 103°08′43″ E	13
Endau, Johor	END	South China Sea	2°39′18″ N, 103°37′24″ E	10
Kuantan, Pahang	KUN	South China Sea	3°48′37″ N, 103°20′09″ E	12
Kuala Besut, Terengganu	BST	South China Sea	5°49′50″ N, 102°33′43″ E	13
Kuala Besar, Kelantan	KB	South China Sea	6°12′21″ N, 102°14′04″ E	16

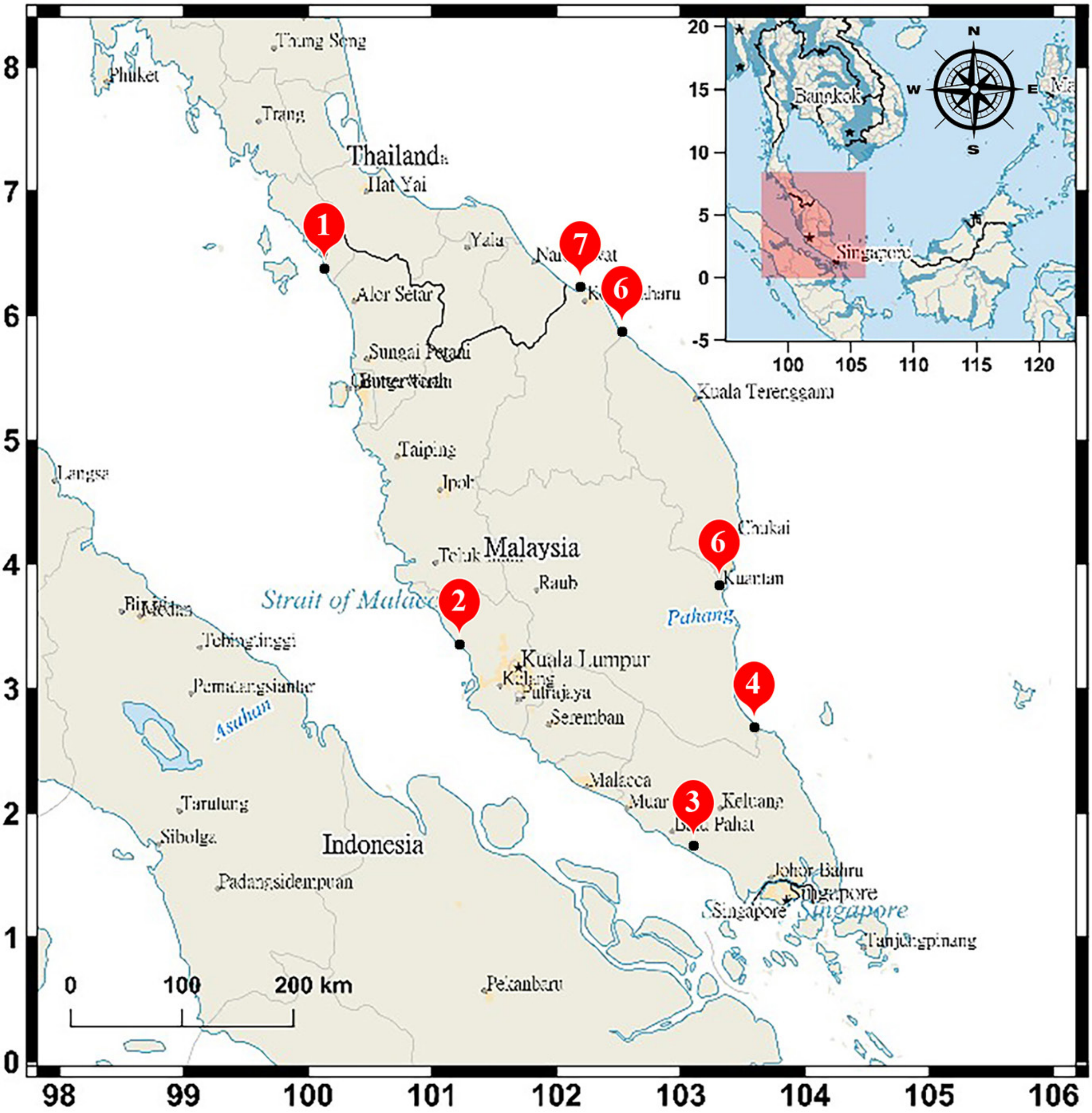

Fig. 1. Sampling locations of *M. hardwickii* along the coastal waters of Peninsular Malaysia.

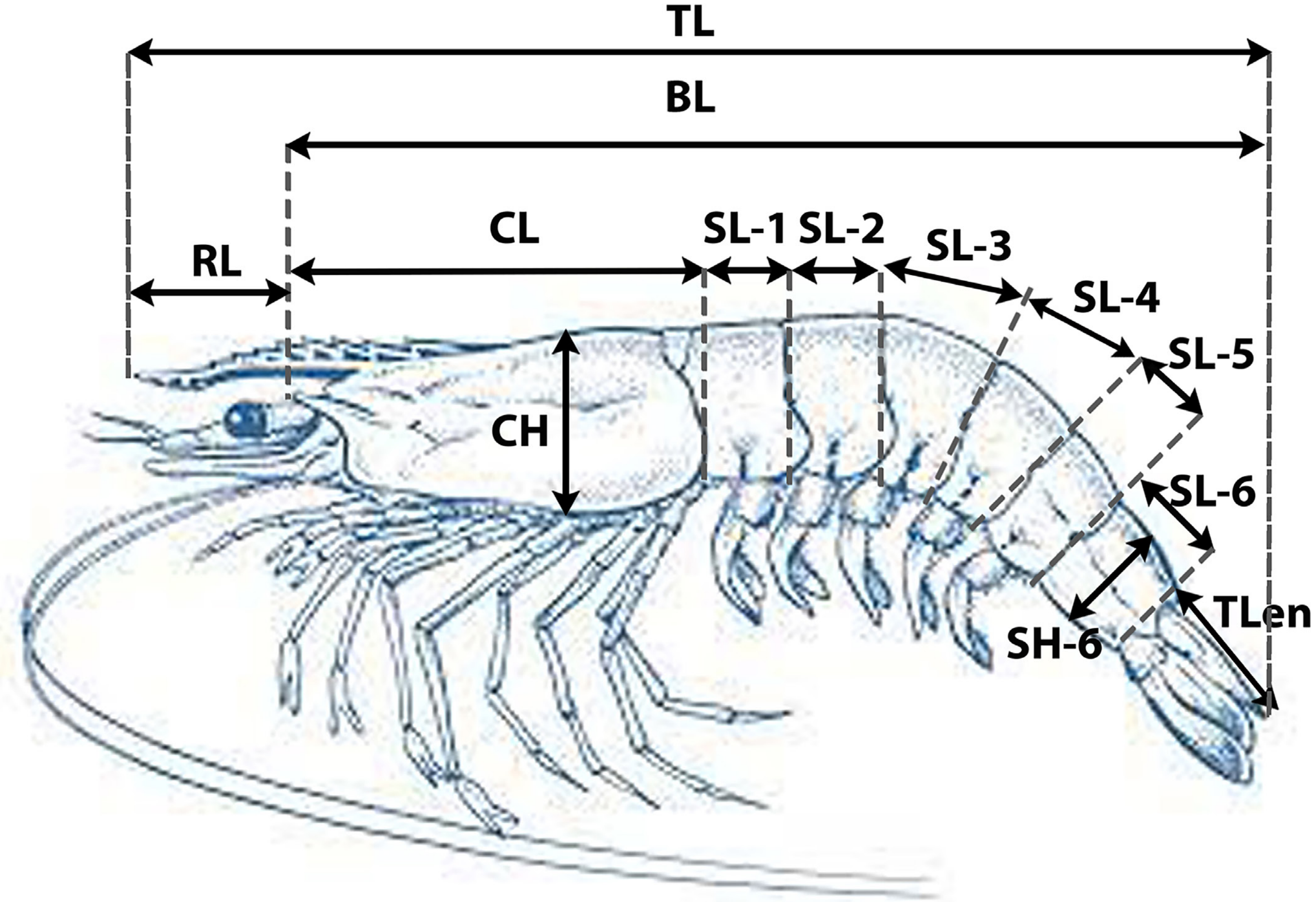

Fig. 2. Traditional morphometric measurements of *M. hardwickii*, modified from Pérez-Farfante & Kensley (1997), Chan (1998), and Parenrengi et al. (2022). TL, Total Length, BL, Body Length; RL, Rostrum Length; CL, Carapace Length; CH, Carapace Height; 1SL, Length of the First Body Segment; 2SL, Length of the Second Body Segment; 3SL, Length of the Third Body Segment; 4SL, Length of the Fourth Body Segment; 5SL, Length of the Fifth Body Segment; 6SL, Length of the Sixth Body Segment; 6SH, Height of the Sixth Body Segment; TLen, Telson Length.

USM_INV362), Kuantan (USM_INV412–USM_INV424), Kuala Besut (USM_INV192–USM_INV204), and Kuala Besar (USM_INV162–USM_INV177).

Traditional morphometric measurements. Character selection was primarily based on the descriptions of *M. hardwickii* by Pérez-Farfante & Kensley (1997) and Chan (1998), with modification following Parenrengi et al. (2022). A total of 12 morphometric characters were selected (Fig. 2). All measurements were conducted using a digital calliper (±0.01mm) and recorded in triplicate to minimise errors.

Truss-network measurements. A total of 21 landmarks were initially digitised on the highest-quality image of each specimen using Thin Plate Splines Utility (TPSUtil) ver. 2.15 and saved in Thin-Plate Splines Digitised (TPSDig) format (Rohlf, 2008). These landmark points were used to represent shape variations among specimens by using TPSDig ver. 2.32, generating a total of 44 distance variables (DV) (Fig. 3, Table 2). To ensure consistency, all specimens were positioned as shown in Fig. 3, as the orientation of the photographed specimens influences the measurement of the abdominal somites. Each specimen was digitised twice to minimise measurement errors (Fruciano, 2016; Halim et al., 2022). Truss-network characters were analysed using MorphoJ (v1.06d) (Klingenberg, 2011).

Statistical analysis. To compare each measurement method (traditional vs. truss-network), we first calculated the classification accuracy using Discriminant Analysis (DA), with a leave-one-out cross-validation procedure. We performed DA to compare *M. hardwickii* populations in two ways; (1) pairwise comparisons, in which each population was compared against another, and (2) an overall comparison using Canonical Variate Analysis (CVA), to assess all populations simultaneously. Traditional morphometric measurements (e.g. body length) were analysed using XLSTAT (v2019, Addinsoft, New York, USA), while truss-network data (landmark-based measurements) were analysed in MorphoJ software. According to Mitteroecker & Bookstein (2011), analyses based on traditional measurement may yield artificially high classification rates as the number of dimensions (variables) increases, potentially leading to inaccurate interpretations by exaggerating populations distinctiveness, even when actual shape differences are minimal. Therefore, DA was carefully applied to the truss-network dataset to ensure more reliable and biologically meaningful classification results.

Table 2. Description of truss-network variables.

Landmarks	Description of variables
LM 1	Tip of the rostrum
LM 2	Posterior of rostral tooth base
LM 3	Dorsal, a point on the first abdominal somite
LM 4	Basal segment of the fifth pleopod
LM 5	Antennal basal segment
LM 6	Tip of the antennal spine
LM 7	Dorsal, a point on the first abdominal somite
LM 8	Basal segment of the first pleopod
LM 9	Dorsal, a point on the second abdominal somite
LM 10	Basal segment of the second pleopod
LM 11	Dorsal, point on the third abdominal somite
LM 12	Basal segment of the third pleopod
LM 13	Dorsal, a point on the fourth abdominal somite
LM 14	Basal segment of the fourth pleopod
LM 15	Dorsal, point on the fifth pleopod
LM 16	Basal, a point on the fifth abdominal somite
LM 17	Dorsal, point on the sixth abdominal somite
LM 18	Basal, a point on the sixth abdominal somite
LM 19	Tip of telson
LM 20	Base of the second rostrum teeth
LM 21	Tip of the gastrofrontal crest

Regression analysis was conducted to examine the relationship among morphometric characters and to determine which morphometric characters significantly contributed to the morphological differences between *M. hardwickii* populations (Basuonie et al., 2020). Both univariate ANOVA and independent t-tests were applied to assess the significance of these differences, evaluating the influence of individual traits across population groups. All statistical analyses were performed using SPSS Statistics version 27. To correct for size effects, traditional measurement data were log-transformed following Klingenberg (2016), to allow scale-independent comparisons and to improve accuracy of morphometric variation estimates (Klingenberg, 2016; Glazier, 2021). In addition to comparing both approaches, we leveraged the advantages of the truss-network method by analysing and visualising shape differences among *M. hardwickii* populations. All analyses were based on the right-side configuration used in the truss-network measurements. To enhance interpretability, the configuration points were reflected to create symmetrical "shrimp-like" visualisations (Fruciano et al., 2011).

Principal Component Analysis (PCA) was performed using PAST version 4.03 (Hammer & Harper, 2001) and MorphoJ software (Klingenberg, 2011) to visualise shape variation among *M. hardwickii* populations. PCA was preferred over Canonical Variate Analysis (CVA) for illustrating shape differences, as it generates ordinations that provide clearer and more accurate representations of morphological variations (Boulesteix, 2005; Mitteroecker & Bookstein, 2011). In addition, PCA outputs are useful for identifying clusters corresponding to different populations (Bookstein, 1997; Claude, 2008). The significance of the principal components (PCs) was determined based on their contribution to total variation, with components contributing more than 5%

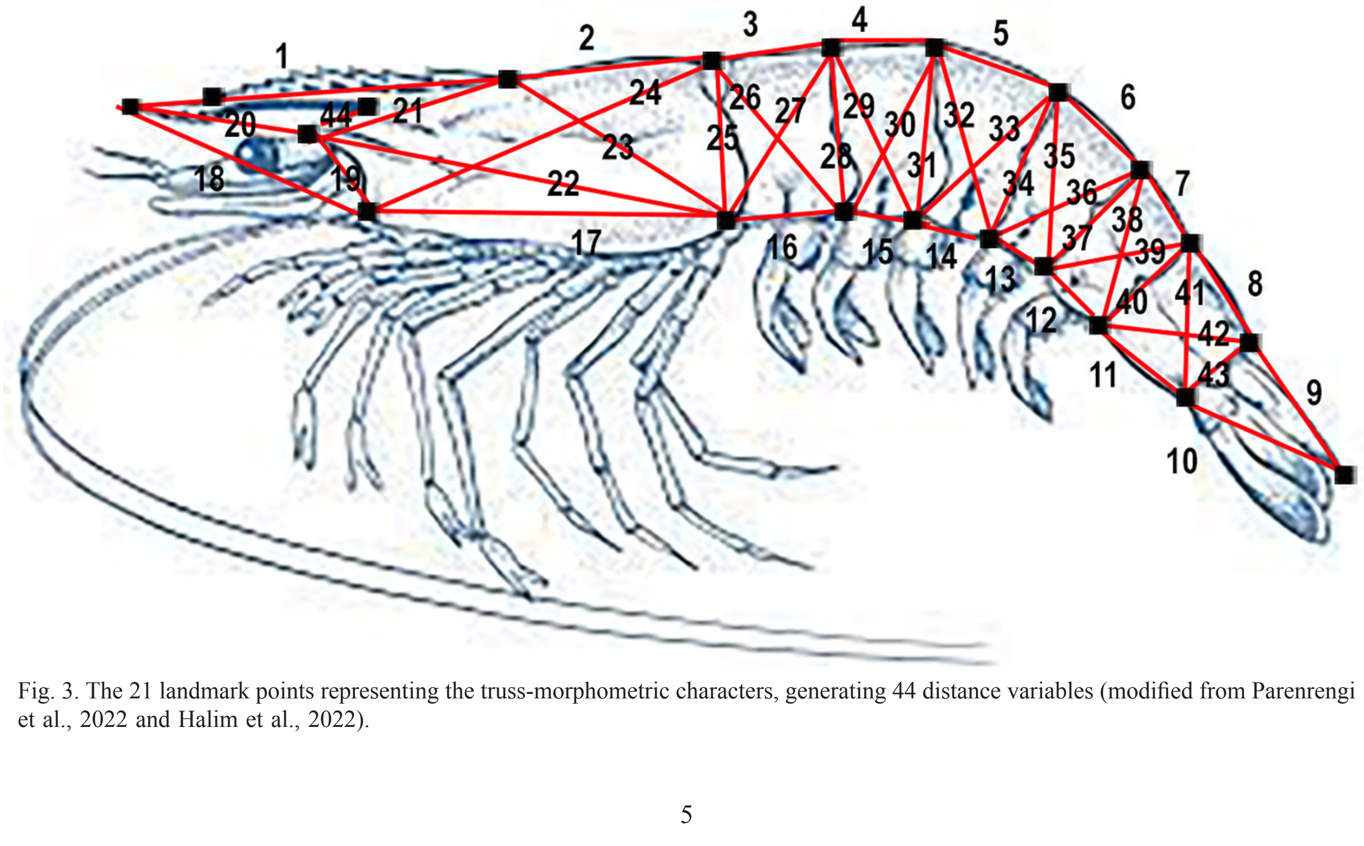

Fig. 3. The 21 landmark points representing the truss-morphometric characters, generating 44 distance variables (modified from Parenrengi et al., 2022 and Halim et al., 2022).

Table 3. Cross-validated correct classification rates for traditional and truss-network morphometric methods. The bold values show the minimum and the maximum classification rates (%) observed amongst the different populations. BP = Batu Pahat, END = Endau, BST = Kuala Besut, PRL = Kuala Perlis, SEL = Kuala Selangor, KUN = Kuantan, and KB = Kuala Besar.

Morphometric measurement	**Discriminant analysis of *M. hardwickii* populations (canonical variate analysis)**							
	Mean value (%)	**BP**	**END**	**BST**	**PRL**	**SEL**	**KUN**	**KB**
Traditional	73.95	69.23	70.0	92.30	60.0	**42.85**	83.33	**100.0**
Truss-network	85.91	88.88	**77.5**	85.39	88.61	88.51	82.64	**89.84**

considered significant (Sherratt et al., 2014; Halim et al., 2022). Fruciano et al. (2014) and Franchini et al. (2014) noted that PCA is increasingly utilised in advanced morphometric studies such as truss-network and geometric morphometric analyses, due to its ability to avoid exaggerating separation between *M. hardwickii* populations. Shape differences among populations were observed based on the segregation in the PCA scatterplot and were visualised using wireframe graphs, which depict each population's mean shape relative to the grand mean.

RESULTS

Comparison of morphometric approaches in discriminating *M. hardwickii* populations. Based on CVA, our study revealed notable differences in the correct classification rates between the traditional approach and the truss-network approaches (Table 3). The traditional approach, which employs linear measurements of external shrimp morphology, showed a wide range of correct classification rates, from 42.85% to 100%, with a mean rate of 73.95%. In contrast, the truss-network approach demonstrated better performance, achieving a higher mean classification rate of 85.91%, though within a narrower range of 77.95% to 88.94%. Interestingly, the traditional approach successfully classified all individuals from the Kuala Besar (KB) population into their respective groups (100%), whereas the truss-network approach accurately classified 89.84% of *M. hardwickii* individuals from the same population.

This result demonstrates a degree of consistency between the morphometric approaches in distinguishing *M. hardwickii* populations, although differences in correct classification rates were observed. The truss-network approach yielded higher classification accuracy compared to the traditional method, even after dimensionality reduction was applied on the truss-network dataset. In this case, discriminant analysis (DA) was performed on a subset of principal components. Specifically, the cross-validation classification rate for the canonical variate analysis (CVA) on the truss-network data, including allometric variation was recorded at 85.91% (Table 3).

Morphological differences among *M. hardwickii* populations. The morphological differences among *M. hardwickii* populations are illustrated in Figure 4, with detailed morphometric measurements (minimum, maximum, mean, and standard deviation) provided in Table 4. Principal Component I (PCI) and Principal Component II (PCII) accounted for 52.97% and 28.45%, respectively, of the total shape variation, and together explaining 81.42% of the overall variation. This suggests substantial shape divergence among the populations, which are relatively well-separated in the PCA plot. Two of the twelve morphometric characters that contributed significantly to PCI were the First Body Segment Length (1SL), with a loading of 0.904, and the Third Body Segment Length (3SL) with a loading of 0.313. Meanwhile, three variables with relatively high loadings on PCII were Carapace Length (CL) (0.687), Rostrum Length (RL) (0.446), and Total Length (TL) (0.314). However, RL was excluded from further analysis because ANOVA and Kruskal-Wallis tests showed it was not statistically significant (ANOVA: $F = 0.484$, $p > 0.05$; Kruskal-Wallis: $p = 0.178$). The most influential morphometric characters across both axes were 1SL, 3SL, CL, and TL. This is evident in the biplot, where these variables appear as long vectors aligned closely with PCI and PCII (Fig. 4), indicating strong contributions to shape variation.

The morphometric characters were size-standardised using the residuals from the regression of each character against overall size along both principal component axes. The size-standardised values for the First Body Segment Length (1SL) and Third Body Segment Length (3SL) were positively correlated along PC1. The strength of the association between 1SL and 3SL was particularly distinct along the PC1 axis. Populations with longer 1SL tended to have longer 3SL, and vice-versa with shorter 1SL was associated with shorter 3SL (Fig. 4). The KB and BP populations were distinctly separated from those of KP, SEL, END, KUN, and BST, primarily along the PC1 axis. KB and BP populations formed a cluster on the positive side of PC1, characterised by relatively long 1SL and 3SL (see A.1), while the remaining five populations clustered on the negative side of PC1, exhibiting relatively shorter values for these characters (see A.2).

In contrast, the size-standardised morphometric characters of Carapace Length (CL) and Total Length (TL) were positively correlated along PC2. Each population could be grouped based on this relationship: populations with long CL also had long TL (see B.1), and populations with short CL had short TL (see B.2) (Fig. 4). However, no distinct segregation was observed along PC2, as most individuals from each *M. hardwickii* population were distributed along this axis.

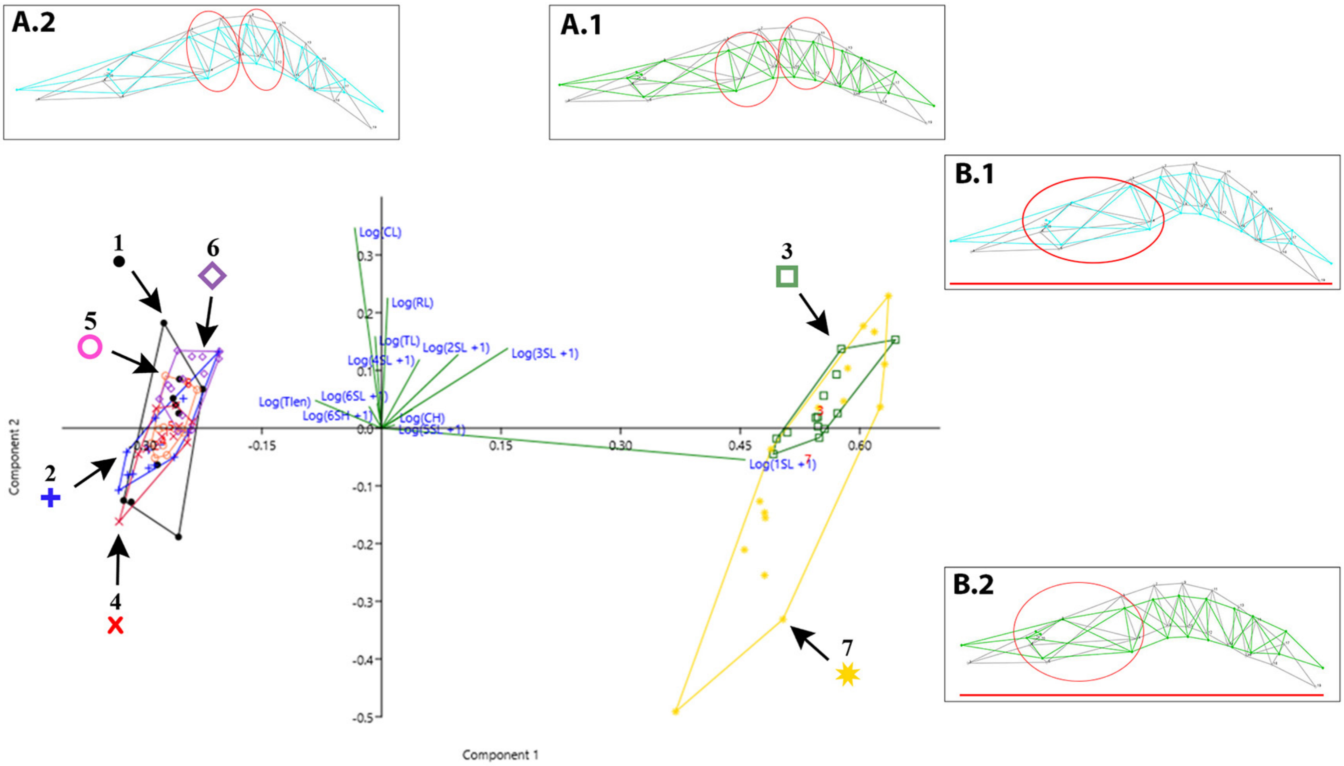

Fig. 4. Principal component plot depicting the two major axes of morphological variation to facilitate visualisation and interpretation of two site assemblages; (1) Kuala Perlis, PRL (black circle shape), (2) Kuala Selangor, SEL (dark blue plus shape), (3) Batu Pahat, BP (green square's line shape), (4) Endau, END (red X shape), (5) Kuantan, KUN (pink circle line shape), (6) Kuala Besut, BST (purple diamond line shape), and (7) Kuala Besar, KB (yellow star shape).

Thus, considering the number of individuals and the projection pattern of each population along PCI and PCII, the segregation pattern in the PCA scatterplot shows that BP and KB populations exhibit clear separation from the other five *M. hardwickii* populations along the PCI axis (Fig. 4). This separation is driven by the notably greater lengths of the first body segment (1SL) and third body segment (3SL) in the BP and KB populations. The morphometric data support this distinction, with both populations recording the highest mean values for 1SL (9.52 in BP and 9.36 in KB) and elevated values for 3SL (12.11 in BP and 13.51 in KB population, respectively) (Table 4). In contrast, the remaining *M. hardwickii* populations (PRL, SEL, END, KUN, and BST) are clustered on the negative side of the PC1 axis, characterised by comparatively shorter 1SL and 3SL. These results demonstrated that the morphological divergence observed in the PCA is consistent with the morphometric measurements, highlighting the unique shape characteristics of the BP and KB populations.

DISCUSSION

Comparison of morphometric approaches in discriminating *M. hardwickii* populations. The present study demonstrates the effectiveness of two morphometric approaches (traditional measurement vs. truss-network) in discriminating *M. hardwickii* populations in the coastal waters of Peninsular Malaysia. Overall, the truss-network approach performed better at the population level, achieving a classification accuracy of 85.91%, making it a more reliable method for distinguishing between populations.

The accuracy of the truss-network approach ranged from 77.95% to 89.84%, indicating a relatively narrow range of performance. This consistency suggests that the truss-network approach is more robust across *M. hardwickii* populations and less affected by external factors compared to traditional methods (Fernando & Amarasinghe, 2014; Azfar et al., 2020). This method is particularly useful for detecting even relatively small, localised shape differences (Klingenberg, 2016), which is important for intraspecific studies (Schmieder et al., 2015). The precision offered by the truss-network approach makes it highly valuable for diverse biological applications, ranging from species discrimination to intraspecific comparisons. Several studies have demonstrated the utility of the truss network method in enhancing classification accuracy and assigning individuals to distinct intraspecific groups (Turan, 1999). For example, an investigation on the giant prawn, *Macrobrachium rosenbergii* (De Man, 1879), in Indonesia revealed that phenotypic mixing within populations ranged from 68.33% to 90.00%, with inter-population differences ranging from 5.00% to 26.67% (Hadie et al., 2002).

Similarly, a study on the Arabian red shrimp (*Aristeus alcocki* Ramadan, 1938), a major commercial fishery species, successfully applied truss morphometrics to differentiate approximately 71.5% of males and 72.1% of females from five populations along the Indian coast into two groups (Purushothaman et al., 2017). In summary, this finding

Table 4. Morphometric measurement of the seven *M. hardwickii* populations. PRL = Kuala Perlis, SEL = Kuala Selangor, BP = Batu Pahat, END = Endau, KUN = Kuantan, BST = Kuala Besut, and KB = Kuala Besar.

Sample	**PRL (n = 10)**	**SEL (n =14)**	**BP (n = 13)**	**END (n = 10)**	**KUN (n = 12)**	**BST (n = 13)**	**KB (n = 16)**
Total length (TL)	6.47–12.21	7.59–9.82	7.88–11.4	8.26–10.15	7.09–11.1	10.06–11.65	9.12–10.52
As percentage of TL							
Rostrum length (RL)	16.99–30.60 (21.94±3.65)	19.28–30.46 (23.48±2.82)	18.82–26.78 (21.74±2.13)	20.40–26.69 (22.83±2.02)	13.81–39.08 (24.57±6.71)	16.38–26.11 (20.67±2.78)	18.26–22.30 (20.19±1.23)
Carapace length (CL)	27.45–35.86 (32.62±2.58)	28.63–41.96 (33.05±4.01)	29.23–42.06 (32.92±3.59)	25.91–34.68 (31.35±2.35)	15.37–33.99 (26.10±5.61)	28.64–32.80 (31.36±1.49)	28.20–34.80 (30.85±2.34)
Carapace height (CH)	13.12–19.61 (15.53±1.82)	12.95–19.89 (15.69±2.03)	12.28–16.88 (14.56±1.21)	13.28–22.88 (16.46±3.29)	7.95–14.66 (10.36±2.05)	12.27–15.31 (13.43±1.00)	13.10–16.16 (14.36±0.96)
First body segment length (1SL)	7.94–9.67 (8.64±0.52)	7.45–14.37 (9.49±1.84)	7.76–12.81 (9.52±1.35)	7.63–10.00 (8.94±0.85)	7.45–9.88 (8.60±0.66)	8.05–10.18 (9.02±0.67)	5.05–13.54 (9.36±1.93)
Second body segment length (2SL)	9.08–17.47 (9.49±1.84)	11.04–17.00 (12.73±1.87)	9.99–12.86 (11.69±0.82)	12.59–16.82 (15.26±1.18)	6.41–13.06 (9.92±1.89)	12.42–14.99 (13.77±0.72)	8.84–11.07 (10.18±0.72)
Third body segment length (3SL)	7.73–10.73 (9.63±0.76)	8.76–13.83 (10.41±1.50)	8.44–12.98 (12.11±2.17)	9.93–12.01 (11.10±0.77)	5.05–12.09 (9.19±2.06)	9.36–11.22 (10.29±0.59)	12.36–14.59 (13.51±0.69)
Fourth body segment length (4SL)	5.00–9.27 (10.13±1.26)	6.26–72.30 (12.00±17.37)	5.44–7.61 (6.66±0.68)	6.01–9.69 (7.16±1.03)	5.73–12.41 (9.25±2.19)	4.89–7.45 (6.58±0.82)	10.47–12.50 (11.21±0.61)
Fifth body segment length (5SL)	6.06–9.74 (7.91±1.02)	6.48–9.63 (7.84±0.92)	6.23–9.01 (7.28±0.80)	6.21–10.29 (7.78±1.20)	6.31–89.90 (13.62±20.37)	5.24–7.97 (6.92±0.89)	5.35–7.90 (6.82±0.70)
Sixth body segment length (6SL)	9.89–14.68 (11.05±1.34)	9.77–12.38 (10.76±0.74)	9.88–12.00 (10.63±0.72)	9.86–12.03 (10.59±0.64)	4.25–11.57 (6.85±1.70)	8.94–11.14 (10.37±0.61)	9.44–11.61 (10.48±0.63)
Sixth body segment height (6SH)	9.79–14.53 (10.60±1.42)	9.40–11.76 (10.24±0.76)	8.69–11.70 (10.20±0.90)	9.32–12.03 (10.21±0.74)	2.71–7.67 (4.61±1.44)	8.66–11.11 (9.96±0.63)	8.39–10.52 (9.34±0.69)
Telson length (Tlen)	10.95–15.71 (13.02±1.49)	11.61–19.60 (15.04±2.39)	11.55–18.67 (15.49±2.02)	12.70–17.28 (14.58±1.19)	4.61–14.04 (10.04±2.20)	11.78–15.37 (13.17±1.06)	12.34–15.90 (14.48±1.31)

Table 5. Factor loadings (correlation between original morphometric characters and PC axes) for PCI and PCII. See Fig. 4, and Fig. 2, Fig. 3 and Table 2 for measurements and variable definitions.

	PC1	PC2
Log (TL)	-0.016	***0.314**
Log (RL)	0.015	****0.446**
Log (CL)	0.067	****0.687**
Log (CH)	0.076	0.064
Log (1SL + 1)	****0.904**	-0.108
Log (2SL + 1)	0.189	0.252
Log (3SL + 1)	***0.313**	0.274
Log (4SL + 1)	0.094	0.234
Log (5SL + 1)	0.032	0.010
Log (6SL + 1)	-0.010	0.083
Log (6SH + 1)	-0.030	0.073
Log (TLen)	-0.164	0.095

Note: Highlight for each axes; ** highest morphometric character loading, *moderate morphometric character loading

collectively demonstrated that advanced morphometric approaches, particularly the truss-network system, are highly effective and reliable for detecting subtle morphological differences, classifying individuals into distinct intraspecific groups, and overcoming the limitations of traditional morphometric approaches. As such, this approach offers a powerful framework for taxonomic resolution, stock discrimination and fisheries management.

While traditional methods were somewhat effective, their classification accuracy ranged from 42.85% to 100%, with a mean of 73.95%. This indicates that, despite their overall utility, the traditional approach lacks consistency and reliability in accurately classifying populations across different scenarios (Christodoulou et al., 2018). The wide range of classification accuracy suggests that although this approach may perform reasonably well on average, it is less reliable for producing consistent results in population discrimination (Christodoulou et al., 2018). A traditional morphometric analysis using 10 morphometric characters in the northern shrimp (*Pandalus borealis* Krøyer, 1838) yielded comparable results (Jónsdóttir et al., 2016). Approximately 42% to 79% of 1-year-old *P. borealis* and 41% to 57% of 2-year-old individuals showed similar classification patterns, supporting the finding of this present study.

Although the truss-network system has shown greater precision and consistency in classifying *M. hardwickii* populations, both morphometric approaches serve complementary roles in morphological studies. Traditional morphometric measurements, despite their broader range (42.88% to 100%) and lower accuracy (73.95%), remain valuable for capturing general body proportions and providing baseline morphological data essential for taxonomic and ecological assessments (Jónsdóttir et al., 2016; Christodoulou et al., 2018). Meanwhile, the truss-network systems enhance resolution in detecting localised shape differences, with classification accuracy ranging from 77.95% to 89.94%, demonstrating its robustness and consistency across *M. hardwickii* populations (Fernando & Amarasinghe, 2014; Klingenberg, 2016; Azfar et al., 2020). The synergy of these morphometric methods has been demonstrated in various aquatic species, where traditional measurements provided foundational taxonomic insights, while truss-network systems enhanced population discrimination and sex differentiation (Hadie et al., 2002; Purushothaman et al., 2017; Pasisingi et al., 2024). Integrating both approaches allows researchers to leverage their respective strengths, thereby offering a more comprehensive and reliable framework for species discrimination, population structuring and fisheries management.

Morphological divergence and adaptive significance among *M. hardwickii* populations. Principal Component Analysis (PCA) was used to investigate patterns of dissimilarity in the multivariate dataset. This analysis revealed significant morphological diversity among *M. hardwickii* populations. The results of the present study indicate that morphological differences exist among *M. hardwickii* populations along the coastal waters of Peninsular Malaysia. Although this study did not evaluate the functional (biological or ecological) significance of these morphological differences, the correlations between various morphometric traits in PCI and PCII may offer valuable insights. Therefore, the findings of this study align well with previous descriptions of phenotypic variability in *M. hardwickii* from nearby regions, including the East China Sea and the Taiwan Strait (Tzeng, 2004).

The major axis of shape variation in this study (PCI axis) was strongly influenced by the body segments, specifically the first and third somites (1SL and 3SL), which are critical for locomotion in *M. hardwickii* and other penaeid shrimp. These two segments play a coordinated role in swimming, maintaining stability, and enabling rapid escape responses (Mellon, 2017; Connor & Webster, 2023). The body segments are integral to locomotor activities such as escape behavior, due to their connection with motor giant axons that rapidly transmit signals to the musculature for tail-flipping (Mellon, 2017). Connor & Webster (2023) further suggested that body segmentation in shrimps is evolutionarily optimised for hydrodynamic efficiency during rapid escape maneuvers. Thus, PCI may be associated with defensive mechanisms in response to predator encounters.

In this context, the clear separation of the Batu Pahat (BP) and Kuala Besar (KB) populations along the positive end of PCI can be attributed to their distinctly longer 1SL and 3SL values. These extended segments may provide enhanced swimming thrust and manoeuvrability, offering adaptive advantages in habitats subject to stronger currents or higher predation pressure from demersal fish species common in their habitats (e.g., coastal waters, estuaries and mangrove swamps). In contrast, the remaining populations were clustered on the negative end of PCI, corresponding to shorter segment lengths, possibly indicating reduced exposure to such selective pressures. This population-level segregation along PCI therefore likely reflects the idea that morphological divergence in *M. hardwickii* populations is shaped by ecological pressures specific to their regional environments.

Ecological disparity influenced the morphological differences. The separation of the BP and KB populations from the other *M. hardwickii* populations based on differences in body segment lengths (1Sl and 3SL), likely reflects ecological variation across different marine environments, warranting further ecological studies. These morphological distinctions, particularly in the first and third body segment lengths, may be shaped by local environmental pressures and habitat characteristics specific to each region.

Batu Pahat is located on the western coast of Peninsular Malaysia, facing the Strait of Malacca, a semi-enclosed, shallow body of water that connects the Andaman Sea to the South China Sea. This region is experiences strong seasonal monsoon influences from the Southwest and Northeast monsoons, which significantly affects water currents and tides (Ibrahim & Ismail, 2011; Rizal et al., 2012; Hidayat et al., 2024). Oceanographic studies have shown that the Batu Pahat area is characterised by strong tidal amplification and semidiurnal currents, driven by a sea-level gradient between the Andaman Sea and the South China Sea (Mohtar et al., 2017; Ezuan'izam et al., 2025). These dynamics create high-energy hydrodynamic conditions, with strong currents (up to ~1m/s), elevated turbidity, and suspended sediment concentrations dominated by silty-clay and sandy fractions.

In contrast, Kuala Besar opens into the South China Sea, which is known for more complex hydrodynamic regimes, stronger seasonal thermohaline gradients, and broader salinity ranges (Afifah et al., 2015; Al-Qadami et al., 2025). The region is influenced by monsoonal wind forcing, geostrophic circulation, and eddy formation, resulting in a stratified upper mixed layer and variable salinity. Although specific studies on Kuala Besar are limited, the broader oceanographic characteristics of the South China Sea suggest more dynamic and variable environment conditions compared to the Strait of Malacca. Ecological differentiation between these two marine systems is likely driven by distinct hydrodynamic, salinity, and sedimentation profiles, which may underlie the morphological divergence observed in *M. hardwickii* populations. These differing oceanographic conditions likely promote local adaptation. For instance, longer body segments, as observed in the KB and BP populations, may enhance swimming efficiency in areas with stronger currents or higher sediment loads.

Similar patterns of morphological adaptation to hydrodynamic environments have been reported in other penaeid shrimp and marine crustaceans (Vogt, 2013; Mogdans, 2019; Zhu et al., 2023; Mohale et al., 2024), reinforcing the hypothesis that shape variation is ecologically driven. Furthermore, habitat heterogeneity such as estuarine complexity, turbidity, and substrate composition, may influence morphological traits through selective pressures related to locomotion and predator avoidance. The PCA results suggest that traits like 1SL and 3SL are potentially adaptive responses to local environmental variables, consistent with previous findings that ecological gradients can strongly shape phenotypic divergence in crustaceans (Vermeiren et al., 2020). These insights underscore the importance of integrating ecological parameters with morphometric and genetic analyses for accurate stock assessment and sustainable fisheries management (Mahfuj et al., 2022).

Implications of stock assessment based on morphometric data analysis. Stock selection can be justified by integrating both quantitative and qualitative evidence (Kagainis, 2015). The combination of traditional morphometric measurement and truss-network systems offers a valuable insight into morphological differences among *M. hardwickii* populations along the coastal waters of Peninsular Malaysia. In this study, the identification of two distinct morphological groups provides a potential basis for defining management stocks.

PCA scatterplots and wireframe visualisations revealed clear morphological differentiation, suggesting possible ecological adaptation or evolutionary divergence. These shape differences warrant further investigation to determine their adaptive relevance (Volckaert, 2013). The findings indicate that the stock structure of *M. hardwickii* across the Strait of Malacca and the South China Sea can be effectively described through PCA-based scatterplots and wireframe visualisations. Quantitative analyses and visual outputs collectively support the recognition of stock-specific units, with the Batu Pahat and Kuala Besar populations forming one distinct group, and the other five populations, characterised by shorter body segments comprising another stock unit. This observed segregation may be ecologically driven, highlighting the need for dedicated ecological studies.

Previous research has demonstrated that morphology often correlates with ecological factors when properly evaluated (Webb, 1984; Ehlinger & David, 1988), suggesting that predictive relationships can be established. This study provides a foundation for such investigations. Future research that integrates multivariate morphometric analyses with genetic and environmental data will further refine stock identification and support more effective conservation and fisheries management strategies (Mahfuj et al., 2022).

Since Malaysian fisheries exploit a mix of shrimp species, including *M. hardwickii*, in specific fishing grounds, stock identification remains a challenge. This highlights the need for interdisciplinary approaches in stock assessments, as each discipline offers unique insights into the primary drivers of variability within species and populations. More accurate stock identification will enhance our understanding of stock structure and the mechanisms behind it (Lishchenko & Jones, 2021). However, sampling constraints, such as small or uneven sample sizes, may limit the robustness of the conclusions. Expanding sampling efforts, considering seasonal or lifestage variations, and incorporating studies on functional morphology could further improve our understanding of the adaptive significance of shape differences.

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