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# Describing the Body Shapes of three populations of *Sardinella lemuru* (Bleeker, 1853) from Mindanao Island, Philippines Using Relative Warp Analysis

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## Abstract

*This study utilized landmark-based geometric morphometrics to determine and describe the body shape variation of Sardinella lemuru populations collected from the bays of Butuan City, Dipolog City, and Pagadian City in Mindanao, Philippines. A total of 30 males and 30 females from each sampling site were digitized and landmarked using 18 landmark points in the fish's body. Relative warps (RW) for within and between populations were obtained. Significant results for variation between sexes were emphasized by multivariate analysis of variance (MANOVA), canonical variate analysis (CVA), and discriminant function analysis (DFA). RWs show that females exhibit body shapes that are geared to support large number of eggs (i.e. distended belly area) ensuring successful reproductive rate while males exhibit a more slender body and are generally smaller than females. Significant differences were also observed between populations of S. lemuru which can be attributed to geographic isolation permitting little to no interaction between populations. Environmental factors, overfishing/overexploitation could also be considered as factors influencing these morphological variations. Hence, this study showed that landmark-based geometric morphometric methods is an effective tool in describing body shape variations that exist within and between populations of S. lemuru. This initial method in distinguishing between populations is important in proper management of these species.*

**Keywords**: *Sardinella lemuru*, Geometric morphometrics, relative warps, sexual dimorphism, overfishing/ overexploitation, geographic isolation.

## Introduction

Sardines belong to Family Clupeidae, Subfamily Clupeinae. They have a compressed, silvery, streamlined body, protruding scales, and a single soft-rayed dorsal fin. They have a two-lobed non-functional lung and are known for their oily flesh[1]. Having an average small size, they inhabit shallow depths of coastal water or at times in estuaries. They are widely distributed across the globe both on temperate and tropical marine areas where they feed mainly on planktons and thrive through large schools[2]. In the Philippines, they are locally known as *tamban*. Sardines in the Philippines form shoals in coastal waters over the continental shelf where depth is less than 200 meters[3].

*Sardinella lemuru* is one of the top ten most important species in terms of commercial fishing in the Philippines[4]. Since the 1950's, sardines comprised the largest proportion of landed catch in the Philippines[5] and consequently are the most accessible source of protein for millions of Filipinos[3]. Important economic uses of *S. lemuru* aside from being consumed as fresh fish, they are also processed for fishmeal, canning, and also dried for consumption. The ones used for canning are those high quality lager-sized fish, while smaller, along with spoiled bigger fishes, are processed for fishmeal. Ecologically, sardines are basally positioned in a food web that supports pelagic tuna and mackerel, as well as numerous sea birds and marine mammals[3]. Despite its economic and ecological importance, only a few studies on Philippine sardines, with emphasis on its diversity, were done and only a little of these are published. Stock information is scarce and the data are outdated, with the exception of the fish's catch statistics. However, several assessments on stocks determined that the fishery was overfished[6]. A review of the sardine stocks in the Philippines at the national level appear to be healthy, however certain areas started to show signs of depletion particularly sardines in the western and central Visayas based on the data from National Stock Assessment Program (NSAP)[3]. These sardines have been reported to be under heavy fishing pressure in particular, with stocks of *S. gibbosa, S. fimbriata*, and *S. lemuru* being overexploited[7]. This evidence of overexploitation is justified by standard length data of captured fish which is currently less than the standard length at first maturity for the above mentioned species.

Since all fish species have already established their genetic adaptations to the present environmental conditions before serious exploitation, such current, drastic effects of exploitation can totally affect their life-history patterns[8]. In other words, fishing not only decreases the abundance of fish, but also changes their genetic composition[8]. Hence, change in genetic composition influences change and/or variation in the phenotype, and thus morphology of the individual. In light of this, it is the aim of this study to investigate on the different body shape variations that could be occurring within and between the three different populations (i.e. geographically isolated) of *S. lemuru* through the use of landmark based geometric morphometric analysis. This is important since body shape gives an idea to the different adaptations developed by the fish in a particular environment and for stock assessment as well. A study conducted found significant morphological variation in body shapes between sexes of the white goby (*Glossogobius giuris*) using geometric morphometric analysis[9]. Another study regarding morphological variation as well as sexual dimorphism was observed in *Hypseleotris agilis* also by the use of the same method[10]. Geometric morphometric analysis also proved to be successful in describing morphological variations within and among populations in a species of golden apple snail (*Pomacea canaliculata*)[11].

Butuan Bay, Dipolog Bay, and Pagadian Bay are areas in Mindanao, Philippines where *S. lemuru* is widely fished, and probably overexploited. Additionally, it is important to study body shape since it gives an idea on the examination of *S. lemuru*'s evolution in these three areas. Body shape affects efficiency in locomotion in different environments, especially when fishes are searching for food and in escaping predators. Since fishes live in water which is a dense medium, their body shape chiefly influences behavioural performance characteristics, which can also be observed in other aquatic or marine organisms. Thus, body shape variation can tell about behavioural and ecological differences[12]. Moreover, studying body shape is vital for the evolutionary analysis of variation with respect to the environment, among fish populations and allows for theories by emphasizing adaptation to local environmental conditions[13-14]. Therefore, morphometric studies can provide useful information on the evolution of fishes[13,15-20].

## Material and Methods

**Collection of Samples:** *Sardinella lemuru* (figure 2) samples were collected from the bays of Butuan City, Dipolog City, and Pagadian City. There were 30 males and 30 females obtained from each site respectively. Figure 1 below shows the location of the three sampling sites. The specimens were processed right after they were gathered since this species of fish can be easily damaged. Sex was determined through a thorough examination of the fish's gonads. The samples were kept in ice buckets for preservation and then image acquisition followed. These images were then used for morphometric analysis.

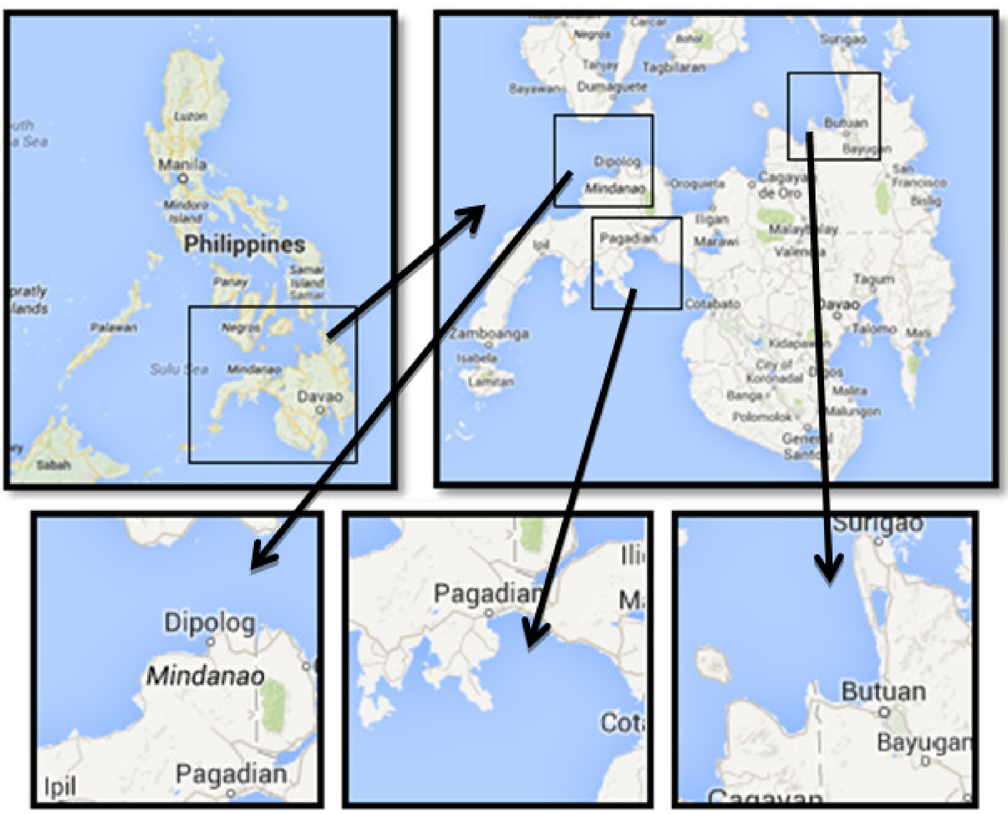


**Figure-1**
**Sampling sites (Butuan City, Dipolog City, Pagadian City) with reference to the whole archipelago of the Philippines. (Source: www.maps.google.com)**

**Image acquisition:** A DSLR (Nikon D5100) camera was used to capture the image of the specimens. It was mounted on a tripod so as to make the camera stable and to allow uniform focus all throughout the image acquisition process. The samples were placed in a standard position with fins teased so as to show their natural position when swimming, as shown in figure 2. Only undamaged fish samples were included.

**Morphometrics and Statistical Analysis:** Geometric morphometric analysis is done through a phenotypic standpoint to determine the morphological variations or differences related to the history of individuals from different locations with distinguishable environmental conditions. It allows the precise and detailed analysis of shape change and shape variation in organisms on the basis of positions of homologous anatomical landmarks or shapes of outlines[21]. Geometric morphometric methods also allow for the graphic presentation of results for visual display and comparison of shape changes based on measured distances, angles, and ratios.

In this study, body shape among *Sardinella lemuru* species from the bays of Butuan City, Dipolog City, and Pagadian City were examined to assess their variations. This was possible through the aid of Geometric morphometric analysis.

The images were processed through landmark-based morphometrics to analyse body shape variations using Tps Dig freeware 2.12. This image analysis and processing freeware facilitates the statistical analysis of landmark data in morphometrics by making it easier to collect and maintain landmark data from digitized images[22]. There were 18 homologous anatomical landmarks that were used to analyse the body shape of the samples. Figure 2 shows the landmarks that were plotted on the images: 1) anterior tip of snout at upper jaw, 2) most posterior aspect of neurocranium (beginning of scales nape), 3) origin of dorsal fin, 4) insertion of dorsal fin, 5) anterior attachment of dorsal membrane from caudal fin, 6) posterior end of vertebrae column, 7) anterior attachment of ventral membrane from caudal fin, 8) insertion of anal fin, 9) origin of anal fin, 10) insertion of pelvic fin, 11) origin of pectoral fin, 12) – 16) contour of the gill cover, 17) posteriormost portion of maxillary, 18) center of the eye.

The geometric configurations composed of x and y coordinates from the digitized landmarks were transformed first into shape variables prior to executing the statistical analyses of shape variation. Since the images contain shape and non-shape variables resulting from the differences in the orientation and position of the fishes during the image acquisition, Generalized Procrustes Analysis (GPA) was used through TpsRelw software. Relative warps were generated to determine the different body shape variations exhibited by this species of fish. Relative warp scores were subjected to Multivariate Analysis of Variance (MANOVA) which is further supported by Canonical Variate Analysis (CVA) and Discriminant Function Analysis (DFA) using PAST (Paleontological Statistics) software to further analyse the variations existing between males and females, and between the geographical locations from which this species of fish were collected.

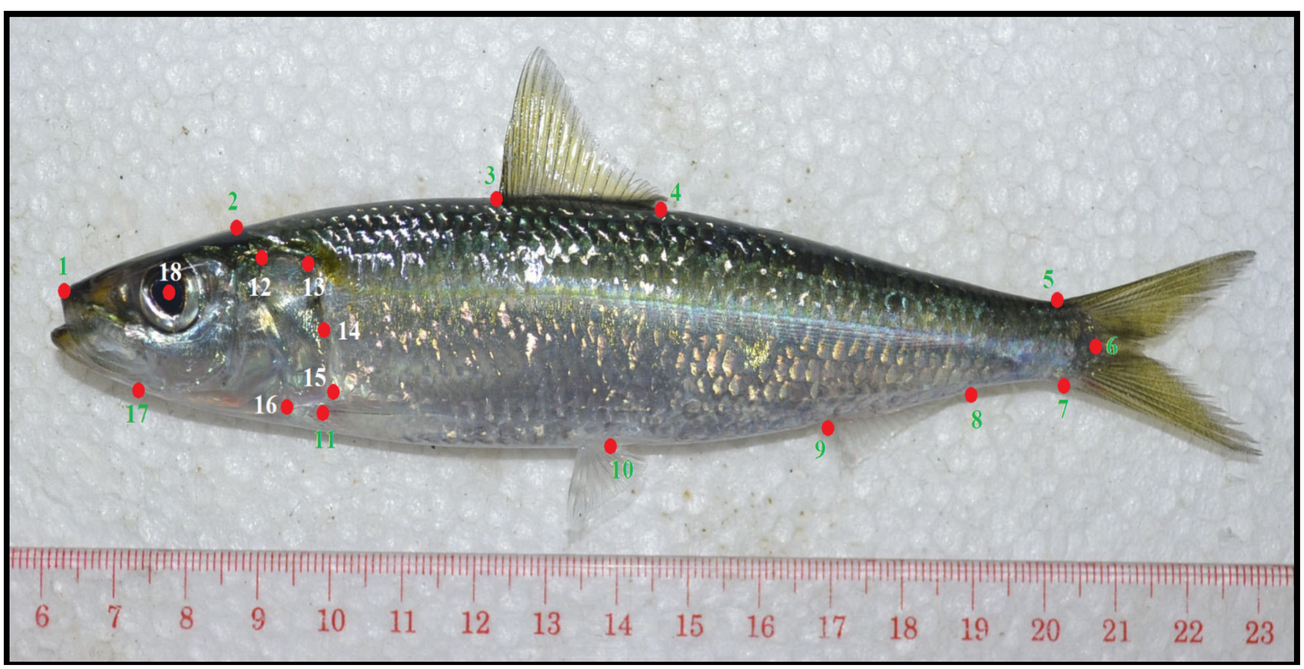


**Figure-2**
**Locations of the 18 landmarks for analysing fish body shape, illustrated as red dots**

## Results and Discussion

The thirty (30) males and thirty females that were collected from each sampling area were subjected to geometric morphometric analysis in order to determine the body shape variation that exists within and between the three populations of *Sardinella lemuru*. It is important to know this aspect of the organism since morphological variations could be attributed to sexual dimorphism and since it is prevalent in the animal kingdom, females and males do not only vary in their reproductive organs but as well as in other external body structures that are not directly linked or associated to reproduction[23, 24]. Knowledge about sexual dimorphism gives an idea on the behavior, ecology, and life history of a particular species which is essential in making comparisons between populations. Another factor that may influence or contribute to these variations existing between sexes and between populations are the effects of overfishing or overexploitaion of this species of fish.

Body shape variation and its pattern is shown and is summarized by the boxplots of the relative warp (RW) scores along with the extremely positive and the extremely negative warps. Figure 3 shows the summary of the variation within the population of female and male *S. lemuru* collected from the bays of Butuan City (a), Dipolog City (b), and Pagadian City (c). The uppermost portion for each figure shows the consensus of the mean body shape from each population. The subsequent table (table 1) contains the descriptions of the shape change of each of the significant warps for each sexes with their variances.

For the Butuan City population (figure 3a), the females exhibit much less variation in the curvature of the body compared to the males .The distension of the mid section in the females is more pronounced than that of the males, while the difference in the length of the ventral and the dorsal side is more or less the same for the two sexes. The female population also exhibits variation in the section between the insertion of the pectoral fin to the insertion of the pelvic fin and also on the part in the posteriormost part of the neurocranium to the origin of the dorsal fin. Variation can also be noticed in the snout region of the female population. The dorsal fin is lengthier in the male population as compared to the females. Table 1 summarizes these variations found in both of the male and female populations from Butuan Bay along with the variances for each relative warp.

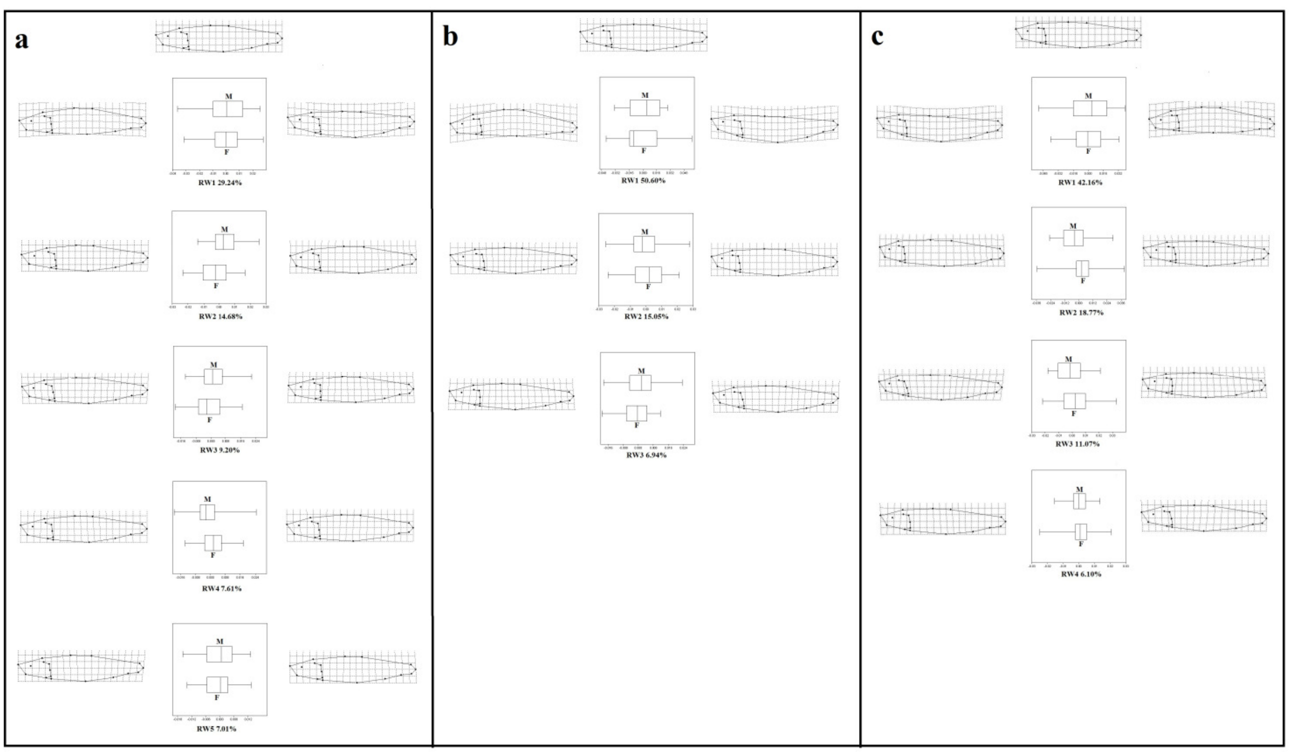


**Figure-3**
**Summary of landmark based geometric morphometric analysis showing the boxplot and variation of the body shapes between sexes of *Sardinella lemuru* females and males from the bays of (a) Butuan City (b) Dipolog City (c) Pagadian City as explained by each of the significant relative warps**

**Table-1**
**Variation in the body shapes of *Sardinella lemuru* populations as explained by each of the significant relative warp and its corresponding percentage variance**

| RW | Female | Male |
|---|---|---|
| | **Butuan City** | |
| 1<br>29.24% | Variation in the curvature of the fish body. The extremely positive warp curves upward as it gets further away from the mean body shape making the dorsal side of the fish look arched, while at the negative extreme, the fish body shape curves at a downward fashion making the ventral side of the fish appear arched upward, somewhat like an inverted U. | Variation on the curvature of the fish's body. The extremely positive warp shows an upwardly curved body, just like a letter U. As it approaches towards the mean, the body curves at a downward fashion, like an inverted U as opposed to the extremely positive warp. |
| 2<br>14.68% | Variation in the compression of the body of the fish at the mid-section. The extremely positive warp shows a rounded mid-section brought about by the outward projection of the part near the belly, and as it reaches the extremely negative side of the warp, the mid-section of the fish's body is slightly compressed towards the middle showing a non-rounded characteristic of the mid-section. | Variation in the compression of the body of the fish at the mid-section. The extremely positive warp shows a rounded mid-section brought about by the outward projection of the part near the belly, and as it reaches the extremely negative side of the warp, the mid-section of the fish's body is slightly compressed towards the middle showing a non-rounded characteristic of the mid-section. |
| 3<br>9.20% | Variation in the difference in length of the dorsal and the ventral side of the body of the fish. The extremely positive warp shows a lengthier ventral side whilst the dorsal side is shorter. The extremely negative warp, on the other hand shows a lengthier dorsal side and a shorter ventral side of the fish. | Variation in the difference in length of the dorsal and the ventral side of the body of the fish. The extremely positive warp shows a lengthier ventral side whilst the dorsal side is shorter. The extremely negative warp, on the other hand shows a lengthier dorsal side and a shorter ventral side of the fish. |
| 4<br>7.61% | Variation in the belly section of the fish. The extremely positive warp shows a lengthier section between the insertion of the pectoral fin to the insertion of the pelvic fin. The length then slowly decreases as it approaches the negative extreme warp. | Variation in the part of the pelvic fin area of the fish's body. The extremely positive warp shows an enlarged area in the pelvis while the extremely negative warp shows a compressed pelvic area. |
| 5<br>7.01% | Variation in terms of the length from the most posterior aspect of the neurocranium to the origin of dorsal fin. From the extremely positive warp, the length increases as it approaches the mean and towards the extremely negative warp which has the longer length of this particular region of the fish. | Variation in the length of the dorsal fin from its origin to the insertion. The extremely positive warp shows a dorsal fin that is shorter and as the relative warp approaches the mean towards the negative extreme, the dorsal fin gains length. |
| | **Dipolog City** | |
| 1<br>50.60% | Variation in the curvature of the body. The extremely positive warp is exhibits a somewhat U shaped curvature and as it approaches the mean towards the extremely negative warp, the fish's body curvature becomes that of an inverted letter U. | Variation in the curvature of the fish's body. The extremely positive warp shows a curvature that is like that of a U shape which is curved upward. The extremely negative warp shows a curvature that is downward, like an inverted U. |
| 2<br>15.05% | Variation in the mid-section area of the fish. The extremely positive warp shows a much wider area in this part of the fish which makes the belly appear distended as compared to the extremely negative warp which shows a compressed belly in the mid-section of the fish's body. | Variation in the mid-section area of the fish. The extremely positive warp shows a much wider area in this part of the fish which makes the belly appear distended as compared to the extremely negative warp which shows a compressed belly in the mid-section of the fish's body. |

| | | |
|---|---|---|
| 3<br>6.94% | Variation in the length of the dorsal and ventral side of the fish. The extremely positive warp shows a lengthier dorsal side and as it gets nearer the mean, the dorsal side shortens and the ventral side gets lengthier approaching the negative extreme warp. | Variation on fish's difference in body length on the ventral and dorsal aspect. The extremely positive warp shows a lengthier dorsal side. As it approaches the mean towards the extremely negative warp, the ventral side gets lengthier while the dorsal side gets lesser in length. |
| | **Pagadian City** | |
| 1<br>42.16% | Variation in the curvature of the fish body. The extremely positive warp curves downward as it gets further away from the mean body shape making the dorsal side of the fish look like an inverted U, while at the negative extreme, the fish body shape curves at an upward fashion making the ventral side of the fish appear like a letter U. | Variation in the curvature of the fish body. The extremely positive warp curves downward as it gets further away from the mean body shape making the dorsal side of the fish look like an inverted U, while at the negative extreme, the fish body shape curves at an upward fashion making the ventral side of the fish appear like a letter U. |
| 2<br>18.77% | Variation in the mid-section area of the fish. The extremely positive warp shows a compressed belly in this part of the fish which makes the belly appear distended as compared to the extremely negative warp which shows a much wider area in the mid-section of the fish's body. | Variation in the mid-section area of the fish. The extremely positive warp shows a compressed belly in this part of the fish which makes the belly appear distended as compared to the extremely negative warp which shows a much wider area in the mid-section of the fish's body. |
| 3<br>11.07% | Fish's difference in body length on the ventral and dorsal aspect. The extremely positive warp shows a lengthier ventral side. As it approaches the mean towards the extremely negative warp, the dorsal side gets lengthier while the ventral side gets lesser in length. | Fish's difference in body length on the ventral and dorsal aspect. The extremely positive warp shows a lengthier ventral side. As it approaches the mean towards the extremely negative warp, the dorsal side gets lengthier while the ventral side gets lesser in length. |
| 4<br>6.10% | Variation on the part starting from the posterior part of the neurocranium to the insertion of the dorsal fin. The extremely positive warp shows a wider area within this part while the extremely negative warp shows a compressed area. | Variation on the part starting from the posterior part of the neurocranium to the insertion of the dorsal fin. The extremely positive warp shows a compressed area within this part while the extremely negative warp shows a wider area. |

In order to show a more definite and significant comparison between the difference of the body shape between the two sexes, Multivariate Analysis of Variance (MANOVA), Canonical Variate Analysis (CVA) and Discriminant Function Analysis (DFA) were done. Table 2 and table 3 contain the summary of the results obtained from the MANOVA and DFA respectively.

Significant differences in body shapes of males and females of *S. lemuru* from the three separate populations were detected which can be clearly seen in the distribution of the samples in the canonical variate axes (figure 4 a, c, and e). Figure 4a elucidates much of these variations between the two sexes and explains the nearly 100% variance within the Butuan population. Figure 4b shows the Discriminant Function Analysis of the pooled scores of both males and females of *S. lemuru* within the same population. The figure further emphasizes the difference between the two sexes showing a minimal overlap of some of the morphological attributes (table 3, Butuan).

For the Dipolog population, figure 3b shows the relative warps of the females and males respectively, with their variances. In this group, the females show a more pronounced body curvature compared to the males. The males also showed much variation in the mid-section of the fish's body compared to the females. Furthermore, much variation can be seen in males in terms of the length in the dorsal and ventral aspect of the body and also in the area near the pelvic fin.

Figure 3c shows the relative warps of the females and males of the Pagadian population. In terms of the curvature of the body, the males exhibit greater variation while the females have greater variation when it comes to the mid-section of the body particularly in the belly part, showing more prominent distension. The females also exhibit greater variation in terms of the length of the dorsal and the ventral side of the body compared to the males. Moreover, the males show much less variation in the distance starting from the posterior part of the neurocranium to the insertion of the dorsal fin. The females show lengthier portion in this part of the body.

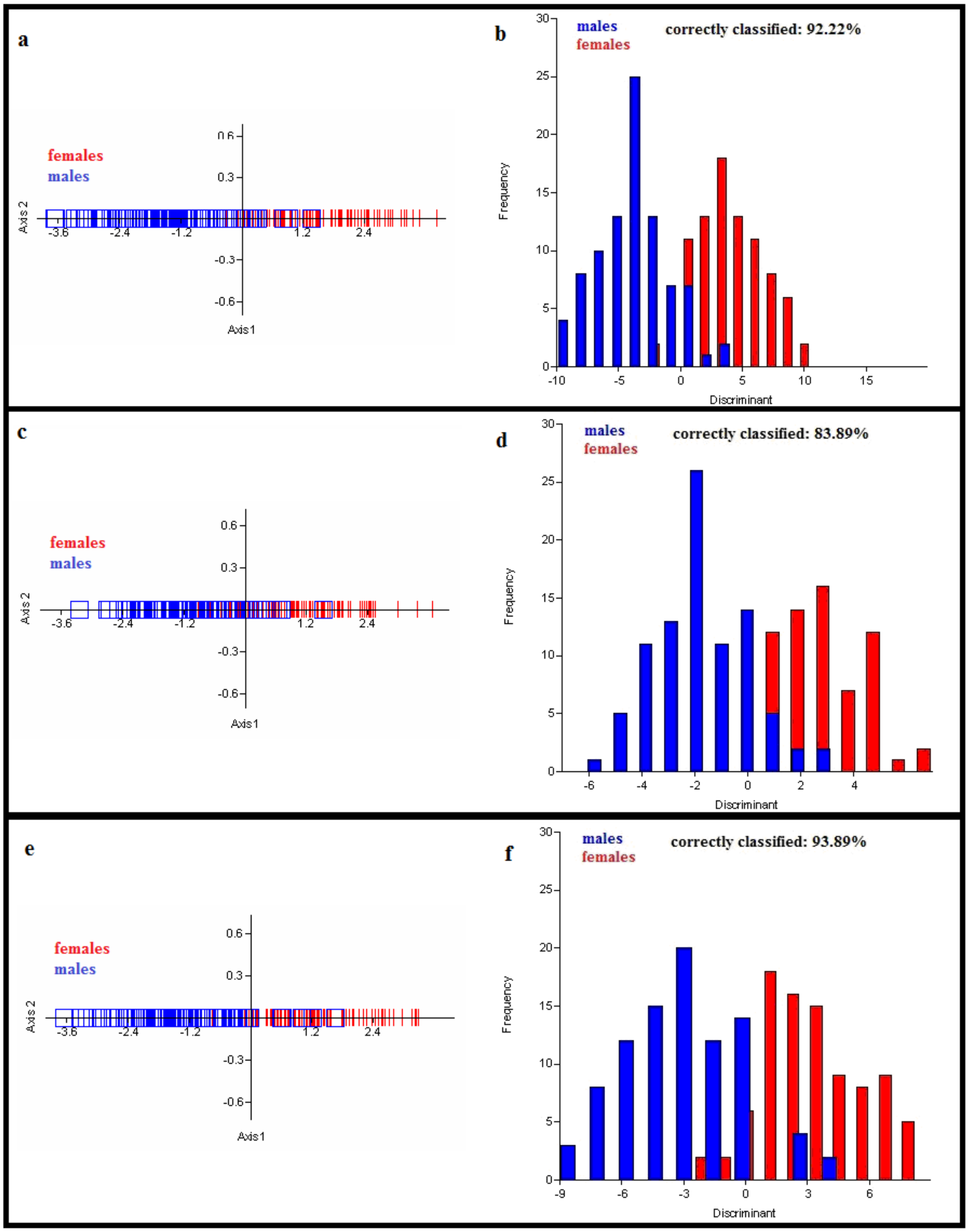


**Figure-4**
**Canonical Variate Analysis (CVA) (a, c, e) and Discriminant Function Analysis (DFA) (b, d, f) plots of the relative scores of *Sardinella lemuru* populations from (a,b) Butuan Bay, (c,d) Dipolog Bay, (e,f) Pagadian Bay**

**Table-2**
**Summary of the MANOVA results for *Sardinella lemuru* in the three different populations.**

| | Butuan | Dipolog | Pagadian |
|---|---|---|---|
| Wilks' lambda | 0.3152 | 0.4705 | 0.357 |
| Pillai trace | 0.6885 | 0.5301 | 0.6439 |
| P-Values | 1.713E-21; 1.509E-21 | 6.706E-11; 6.231E-11 | 4.478E-18; 3.804E-18 |
| Eigenvalue1 | 2.17 | 1.123 | 1.797 |
| Eigenvalue2 | 0.0009056 | 0.001107 | 0.001454 |

**Table-3**
**Summary of the DFA results for *Sardinella lemuru* in the three different populations.**

| | Butuan | Dipolog | Pagadian |
|---|---|---|---|
| P-Value | 5.538E-21 | 1.328E-09 | 7.171E-18 |
| Correctly classified (%) | 92.22% | 83.89% | 93.89% |

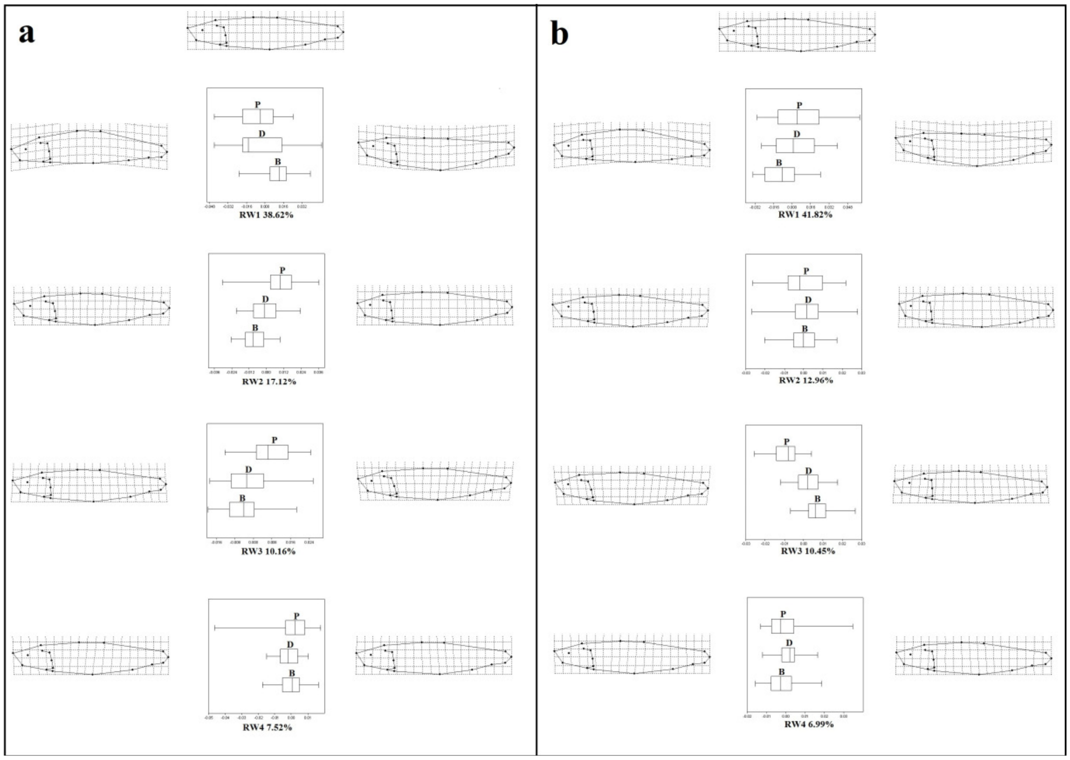


**Figure-5**
**Summary of landmark based geometric morphometric analysis showing the boxplot and variation of the body shapes between populations of *Sardinella lemuru* (a) females (b) males as explained by each of the significant relative warps**

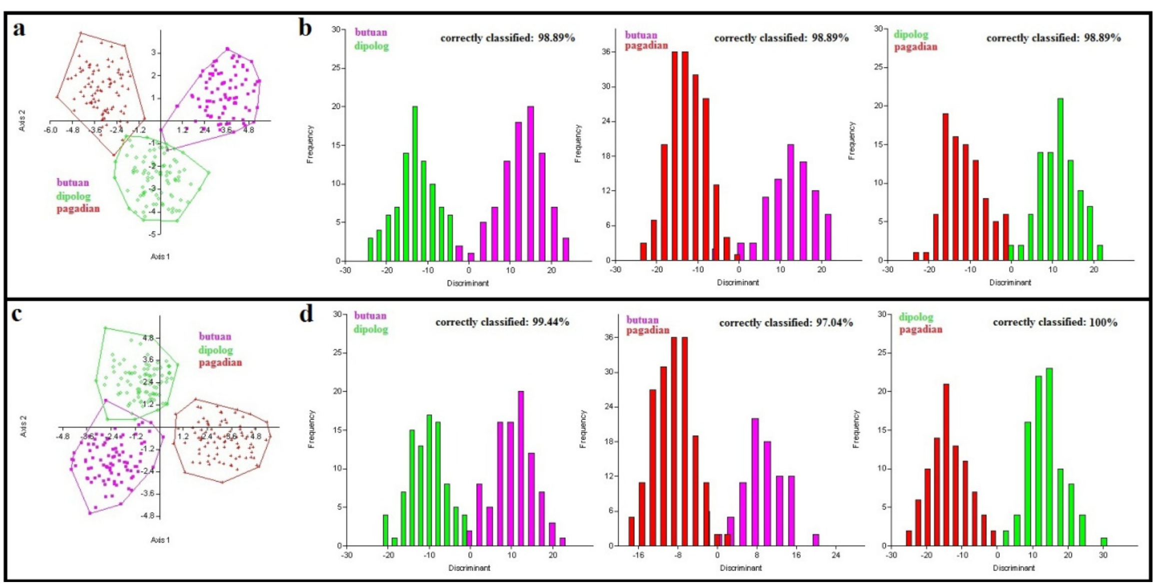


**Figure-6**
**Canonical Variate Analysis (CVA) (a, c) and Discriminant Function Analysis (DFA) (b, d) plots of the relative scores of *Sardinella lemuru* females (a, b) and males (c, d)**

**Table-4**
**Summary of the MANOVA results for *Sardinella lemuru* females and males between the three populations**

| | Females | Males |
|---|---|---|
| Wilks' lambda | 0.02714 | 0.03493 |
| Pillai trace | 1.651 | 1.62 |
| P-Values | 3.04E-141; 3.407E-136 | 6.052E-129; 6.685E-128 |
| Eigenvalue1 | 7.594 | 5.528 |
| Eigenvalue2 | 3.286 | 3.381 |

**Table-5**
**Summary of the DFA results for *Sardinella lemuru* females and males between the three populations**

| | Females | | Males | |
|---|---|---|---|---|
| | P-Value | Correctly Classified (%) | P-Value | Correctly Classified (%) |
| Butuan Vs Dipolog | 5.903E-48 | 98.89% | 1.477E-42 | 99.44% |
| Butuan Vs Pagadian | 1.703E-78 | 98.89% | 1.906E-64 | 97.04% |
| Dipolog Vs Pagadian | 7.866E-45 | 98.89% | 8.779E-50 | 100% |

Pooled relative warps and boxplots between populations and within sexes of the *S. lemuru* were also obtained. Figure 5 shows the summary of the positive and negative extreme warps and the corresponding percentage variance for each sex [females (a), and males (b)]. It shows that females exhibit lesser variation than males in terms of the curvature of the body but the females however, show greater variation in the distension of the belly region. Both sexes show almost the same variation in terms of length of the ventral side of the fish relative to the dorsal side. Females exhibit greater variation in the area from the insertion of the pectoral fin to the insertion of the pelvic fin.

Figure 6 shows the Canonical Variate Analysis (figure 6a and 6c) and Discriminant Function Analysis (figure 6b and 6d) between populations of *S. lemuru* within sexes [females (a, b), and males (c, d)]. Significant differences are shown by the separation of each of the populations in the CVA plot. The CVA plots for both sexes explain the variation existing between the two sexes and could explain for almost 100% of the variance. The Discriminant Function Analysis further emphasizes the difference between populations and within sexes as shown by the minimal overlap of some of the morphological attributes. Table 4 and table 5 contain the summary of the results for MANOVA and DFA between the three populations respectively.

Sexual dimorphism has been tested and shown through the use of Multivariate Analysis of Variance (MANOVA) which suggests that significant sexual dimorphism exists in the overall body shape of the *S. lemuru* species. Wilks' lambda and Pillai trace calculated from this method justifies this result. Moreover, a clearer visualization of the results from MANOVA is shown through Canonical Variate Analysis (CVA). It is one useful tool when it comes to multivariate statistics. This method is utilized to investigate the interrelationship between a number of populations simultaneously with a goal of objectively representing the interrelationships graphically in a few dimensions[9]. It can be seen in the CVA plots presented that the females and males for each population converge or meet around zero along the horizontal axis allowing separation of the two sexes. Therefore, significant differences in body shapes between the sexes of *S. lemuru* for each population were shown by the results of MANOVA and CVA scatter plots.

Looking at the relative warps of each of the sexes in each population and their variances, it can be generalized that the variations occurring in this group of species are mainly on the curvature of the body, compression and decompression at the mid-section of the body particularly in the belly area, the lengthening of the dorsal side relative to the ventral side and vice versa, the length between the insertion of the pectoral fin to the insertion of the pelvic fin and also in the part between the posteriormost aspect of the neurocranium to the origin of the dorsal fin. A slight variation can also be observed at the snout/gape region of the fish. It can be observed that the females exhibit variations that are geared towards body shape that are capable of supporting huge number of eggs (as justified by the more distended belly region compared to the males) while the males exhibit a less distended belly and a more slender body outline. In addition, males are generally shorter than females. A study of female populations of white goby from Lake Buluan showed deeper bodies resulting to stout body outline with greater body curvature compared to the males having a more slender body outline, longer gape length, and caudal peduncle and larger pectoral and anal fin bases[9]. These variations in body shape don't necessarily tell about the phylogenetic history of populations but rather it shows their different adaptations to their present environment[25].

Several factors such as natural selection and sexual selection could result to sexual dimorphism. Significant sexual dimorphic traits were described between sexes of *Hypseleotris agilis* from Lake Lanao, Philippines[10]. They found out that males exhibit bigger head as well as elongated dorsal and anal fin bases which could have resulted from sexual selection or by ecological/niche selection. Sexual dimorphism was observed in body shape of the spotted barb fish (*Puntius binotatus*) with males having slender bodies and wider anal fin bases while females have bigger head region, deeper body depth and shorter tail region, which could be attributed to some selective pressures[26]. Different reproductive roles, niche divergence between the sexes, preference of one sex for particular traits of the other sex, and intra-sexual competition can influence differences in external structures[24, 27-29]. Although sexual dimorphism is apparent in many living organisms, males and females don't only differ in terms of their reproductive organs but as well as in external body structures that are not directly linked or associated to reproduction[23, 24]. In a study on body shapes of threespine sticklebacks (*Gasterosteus aculeatus*), larger females tend to have higher chances of successful reproduction since they produce large number of eggs and are mostly chosen by courting males[30]. Moreover, smaller males tend to have higher advantage over the larger ones, since they can mature and start breeding earlier[24], reside into superior breeding grounds or territories, and finally have higher chances of reproductive success in contrast to the larger males which breed at a later time[31, 32]. Additionally, males tend to have higher reproductive success when they allocate more energy into territoriality, nesting, and parental care, than spending energy to their own growth[30]. Sexual dimorphism could also result from evolutionary and ecological forces wherein the two sexes have different habits conforming their functional adaptations[33]. These ecological forces may provide additional selective pressures for shape differences between sexes[34]. The diversity of an environment can either accentuate or attenuate sexual shape dimorphism[10]. In addition to environmental factors, the genetic make-up of the organism also plays a huge part in the resulting phenotype of the individual.

The results also indicated that there is a clear separation of the three populations based on their morphological differences as what can be seen in the CVA plots in figure 6. This may suggest that geographic isolation or separation could be directly related to the level or degree of phenotypic difference or variation which may indicate that geographic isolation or separation is a limiting factor for the migration between populations or stocks[35]. That is, there is just limited intermingling between the populations. Studies demonstrated that there were clear distinctions in the morphology of *Liza abu* (Heckel, 1842) in the populations from the rivers Orontes, Euphrates, and Tigris[35] and the same observations in the three populations of Anchovy (*Engraulis encrasicolus* L.) in the Black, Aegean, and Northeastern Mediterranean Seas[36]. Fishes are able to respond or adapt to environmental change through their phenotypic plasticity by modifying their physiology and behaviour which eventually lead to variations or changes in their morphology, reproduction or survival that extenuate such forces caused by environmental change[37]. Hence, it could be that *S. lemuru* developed these morphological variations in response to the changes in their environment, or to some selective pressures (e.g. overfishing/ overexploitation, type of fishing gear used, etc.). Fisheries have been described as large-scale uncontrolled experiments in evolution[38, 39] so most likely overfishing and/or the type of fishing gears used are a large contributing factor to these morphological changes. Generally, fishes have greater susceptibility to environmentally-induced morphological variation and in addition, they manifest much variation in morphological attributes both between and within populations compared to other vertebrates[40,41].

## Conclusion

In this study, Geometric Morphometric methods was applied to the three different populations of *Sardinella lemuru* collected from the bays of Butuan City, Dipolog City, and Pagadian City. Through the utilization of modern statistical tools such as Multivariate Analysis of Variance (MANOVA), Canonical Variate Analysis (CVA), and Discriminant Function Analysis (DFA), significant differences in morphology within and between populations was identified in the *S. lemuru* species. Results from the relative warps show that females exhibit body shapes that are geared to support large number of eggs ensuring successful reproductive rate. Males on the other hand exhibit a more slender body and are generally smaller than females. Additionally, variation between populations was also observed which strongly suggests that geographic isolation plays a role as a limiting factor in the migration of the stocks possibly leading to such morphological differences brought about by the differences in the species' environment and selection pressures such as overfishing/overexploitation, and the type of fishing gears used. Thus, this study suggests that landmark-based geometric morphometric method is successful in describing variations that exist within and between populations of the *S. lemuru* species. However, it would be very interesting to study these variations in light of the genes that govern these morphological variations. Knowledge of both phenotypic and genetic aspects of this species of fish would contribute greatly as to the management of the different stocks.

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