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Describing the body shapes of three populations of *Sardinella fimbriata* (Valenciennes, 1847) from Mindanao Island, Philippines using relative warp analysis

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ABSTRACT

Geometric morphometric analysis was used to describe the variations in body shape existing in Sardinellafimbriata sampled from Butuan Bay, Dipolog Bay, and Pagadian Bay in Mindanao, Philippines. A notable degree of significance was detected both within and between populations which is shown by the results obtained from multivariate analysis of variance (MANOVA), canonical variate analysis (CVA), and discriminant function analysis (DFA). Within populations showed sexual dimorphism between the two sexes while geographic isolation may have caused the variations that were detected between the three populations. Additionally, environmental factors such as overfishing/overexploitation and different methods of fishing could also be one of the factors causing these variations. Hence, this study proved the ability of modern geometric morphometrics to distinguish and describe body shape variations existing within and between populations of S. fimbriata. It is recommended, however, that a genetic study regarding these shape variations should be as well conducted to understand more the diversity of this species which would greatly contribute to mananagement strategies of stocks or populations of S. fimbriata.

Keywords: *Sardinella fimbriata*, Geometric morphometrics, relative warps, sexual dimorphism

INTRODUCTION

The Philippines, according to Allen [1] boasts the greatest number of marine fishes, corals [2], seagrasses [3], and marine invertebrates [4] on the planet [5]. Among the fishes found in the Philippine waters are small pelagics which compose about 60% of the total capture fishery production of the country as of 2003 [6]. Included in this fishery is one of the most common sardines, *Sardinellafimbriata*, also known as *fringescalesardinella*. According to a review by Willette and colleagues[7], *S. fimbriata* ranked 6th most common commercially caught fish species by weight and 3rd most common municipally caught fish species based on average annual data from 2004 to 2008. However, the same review indicated that along with other sardines (*S. gibbosa* and *S. lemuru*), *S. fimbriata* faces heavy fishing pressure. Lesser standard length data of captured fish compared to standard length at first maturity proved that such species of fish are overexploited [7]. When one talks about fishing, it could be generalized that it is almost always non-random since gears are designed to select or remove fishes in preference to others, that is, fishes that are bigger in size are most of the time captured [8]. Mortality brought about by fishing therefore provides selective pressure to such population of fish which may cause evolutionary change [8]. Evolutionary change would then suggest change in the genetic structure which is tantamount to changes in phenotype or morphology of the organism. Several studies have already shown that fishing could cause phenotypic evolution in fish stocks [9-12]. In addition, the location of fishing is as well non-random with respect to spatial distribution of stocks since fishing activities would most likely take place in locations where there is greater abundance of fish, where they are most accessible, or both [8]. The bays of Butuan, Dipolog, and Pagadian, are three locations in Mindanao where *S. fimbriata* is present and are probably, widely fished. Taking this into account, it is the aim of the present study to investigate and describe the body shape variations that could be occurring within and between populations of *S. fimbriata* which may be caused by selective pressure due to heavy fishing or overexploitation. This will be made possible through the use of modern tools such as landmark based geometric morphometrics. Several studies already proved the efficacy of geometric morphometrics in describing variations occurring within [13, 14] and between populations [15]. Form change has also been studied in several animal species using geometric morphometrics[16-19]. Studying the body shape variations within and between populations of *S. fimbriata* would reflect their adaptations to their environment in response towards fishing pressure. Additionally, adaptation through natural selection is of course one explanation for phenotypic differences observed between populations, however, differences could also arise through genetic changes from random genetic effects and through environmentally induced variation (which may be caused by overfishing/overexploitation in the present study) [20]. Such was the explanation in the study of adult chinook salmon (*Oncorhynchustshawytscha*) from New Zealand and their source population after 90 years of introduction [20]. Studying this aspect of *S. fimbriata* species would greatly contribute to the betterment of future stock management strategies. This would give knowledge regarding the fish's diversity since there is little to no published work has been done yet regarding this aspect in the species of *S. fimbriata* found in the Philippines.

MATERIALS AND METHODS

Collection of Samples

S. fimbriata(see 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.

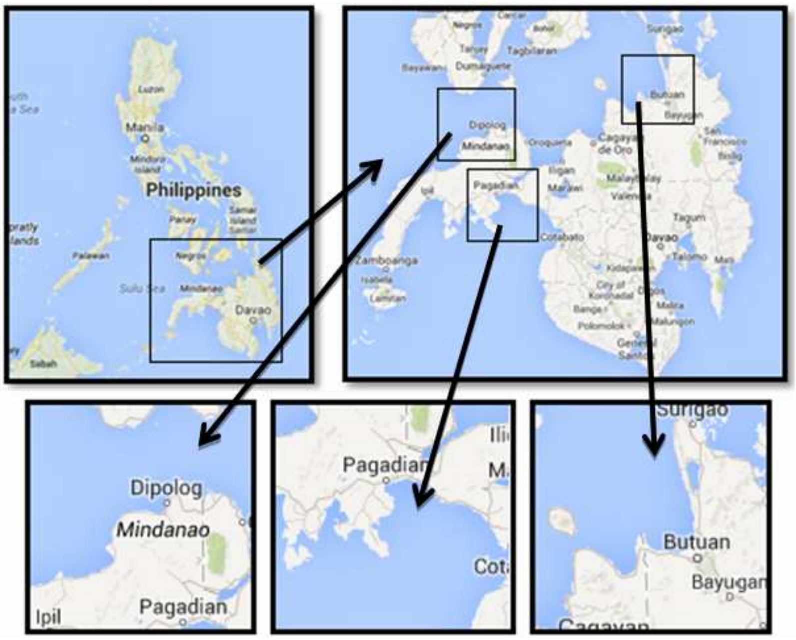

Fig. 1. Sampling sites (Butuan City, Dipolog City, Pagadian City) with reference to the whole archipelago of the Philippines. (Source: www.maps.google.com)

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 carried out from a phenotypic point of view to determine the morphological differences associated with the origins of individuals from different areas with distinct 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 [18]. 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 *S. fimbriata*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 [21]. 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.

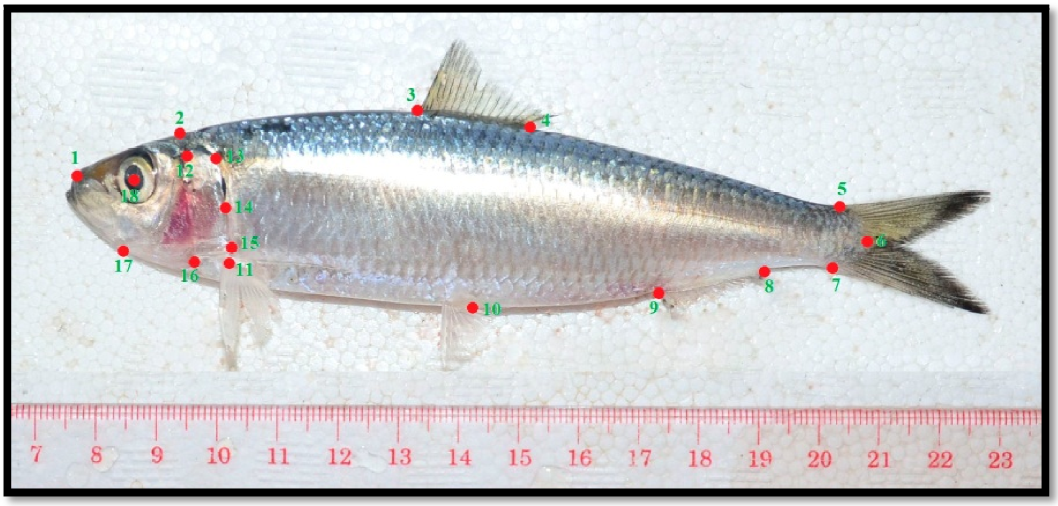

Fig. 2. Locations of the 18 landmarks for analysing fish body shape, illustrated as red dots

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 position and orientation 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

VariateAnalyis (CVA) and Discriminant Function Analysis (DFA) using PAST (Paleontological Statistics) software to further analyse the variations existing between males and females, and also between the geographical locations from which this species of fish were collected.

RESULTS AND DISCUSSION

Geometric morphometric analysis was used to describe the body shape variation that exists within and between populations of *S. fimbriata*. Knowledge about this aspect of the fish is vital since there are several factors that may contribute to the changes that occur in this particular species of fish, such as sexual dimorphism, selection pressures (overfishing, overexploitation, types of fishing gears used, etc.), geographical isolation and many others. Determining sexual dimorphism would give an idea as to the behaviour, ecology, and life history of a particular species which is essential in making comparisons between populations.

The pattern of body shape variation within the population of *S. fimbriata* from the bays of Butuan (a), Dipolog (b), and Pagadian (c) is summarized in Figure 3. Boxplots of the relative warp scores for both sexes are shown together with the positive and negative extreme warps. The uppermost relative warp is the mean body shape for each population. Accordingly, Table 1 contains the description of these variations or shape change for both sexes in each population with their respective variances.

Figure 3a shows the boxplot of the relative warp scores with the variances of both the sexes within the Butuan City population. In here, the females show greater variation when it comes to the curvature of the body compared to the males. The males however, show greater variation in the distension in the mid-section of the body while the females show much variation in the length of the area between the origin of anal fin and insertion of pelvic fin; change in the position of the gill cover, eye, and most posterior aspect of neurocranium. Additionally, the females exhibit dorsal fins that are longer than that of the males.

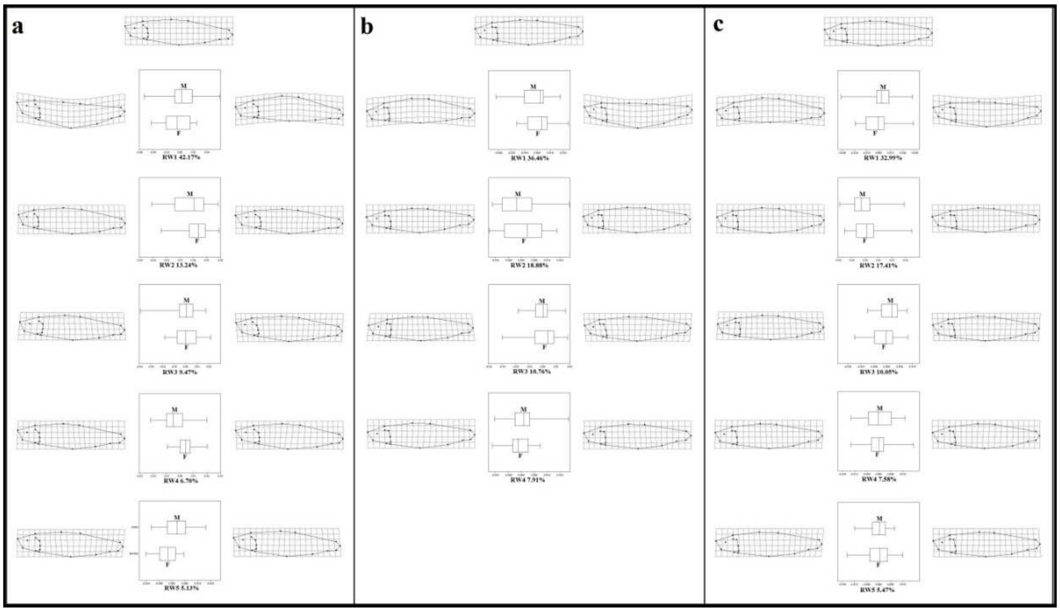

Fig. 3. Summary of landmark based geometric morphometric analysis showing the boxplot and variation of the body shapes between sexes of *S. fimbriata*females and males as explained by each of the significant relative warps.*(a) Butuan Bay population (b) Dipolog Bay population (c) Pagadian Bay population*

For the Dipolog Bay population, Figure 3b contains the box plots of the relative warps and variances of both sexes with the negative and positive extremes. In this population, the males show greater variation the curvature of the body but much less variation in the distension of the mid-section of the body as compared to the females. The females also show a lengthier dorsal fin.

The box plots and relative warps for the Pagadian Bay population is shown in Figure 3c where the females show greater variation in the curvature of the body, and in the distension in the mid-section. The males exhibit lengthier dorsal fin compared to the females.

Table 1. Variation in the body shapes of *S. fimbriata*populations as explained by each of the significant relative warp and its corresponding percentage variance

RW	Female	Male
	Butuan Bay	
1 42.17%	Variation in the curvature of the body. Positive extreme relative warp bends body upward and slightly bends downward approaching the negative extreme from the mean.	Variation in the curvature of the body. Positive extreme relative warp bends body upward and slightly bends downward approaching the negative extreme from the mean.
2 13.24%	Variation in the compression and decompression of the mid section of the body. Positive extreme shows compression while negative extreme shows decompression emphasizing distension of the belly. Change in the position of the gill cover and eye.	Variation in the dorsal and ventral part of the body. Change in the position of the eye and gill cover. Distension just below the gill cover which slowly shifts toward the belly area approaching negative extreme.
3 9.47%	Variation in the position of the caudal peduncle. Change in length of the area between the origin of anal fin and insertion of pelvic fin. Changes in the position of the gill cover, eye, and most posterior aspect of neurocranium.	Variation in the area right after the gill cover and in the area above the anal fin. Change in the position of the anal fin and caudal peduncle. Change in the position of the gill cover, eye and narrowing of the head approaching the negative extreme.
4 6.70%	Variation in the position and length between the origin of anal fin and insertion of pelvic fin. Change in the position of anterior attachment of ventral membrane from caudal fin to insertion of anal fin.	Change in the length from the origin to insertion of dorsal fin; length from the origin to insertion of the anal fin. Change in the position of the insertion of pelvic fin. Change in the position of the eye and gill cover, and posteriormost portion of maxillary.
5 5.13%	Variation in the length from the origin to insertion of dorsal fin. Change in the caudal peduncle. Change in the length between origin and insertion of anal fin.	Change in the position of the eye. Narrowing of the caudal peduncle. Change in length from the origin to insertion of dorsal fin, origin to insertion of anal fin.
	Dipolog Bay	
1 36.46%	Variation in the curvature of the body. Positive extreme relative warp bends body downward and slightly bends upward approaching the negative extreme from the mean.	Variation in the curvature of the body. Positive extreme relative warp bends body downward and slightly bends upward approaching the negative extreme from the mean.
2 18.88%	Change in the position of the eye, gill cover, and origin of pectoral fin. Slight variation in the length between origin and insertion of anal fin. Distension near and above pectoral fin.	Change in the position of the eye, gill cover, and posteriormost portion of the neurocranium. Change in length from origin to insertion of anal fin; from origin to insertion of dorsal fin; and from origin to insertion of pectoral fin.
3 10.76%	Variation in the snout region. Change in the position of the eye and gill cover. Change in length from origin to insertion of dorsal fin and origin to insertion of anal fin.	Change in the position of the eye, gill cover, posteriormost portion of the neurocranium, snout region, and caudal peduncle. Change in length between origin and insertion of dorsal fin, anal fin, and between origin of anal fin and insertion of pectoral fin.
4 7.91%	Variation in the length from origin to insertion of dorsal fin; from origin to insertion of anal fin; and from origin of anal fin to insertion of pelvic fin.	Change in the position of the gill cover. Change in length from origin to insertion of dorsal fin; origin to insertion of anal fin; and from origin of anal fin to insertion of pectoral fin.
	Pagadian Bay	
1 32.99%	Variation in the curvature of the body. Positive extreme relative warp bends body downward and slightly bends upward approaching the negative extreme from the mean.	Variation in the curvature of the body. Positive extreme relative warp bends body downward and slightly bends upward approaching the negative extreme from the mean.
2 17.41%	Variation in the area near pectoral fin and area of the tail approaching caudal fin. Change in the position of the eye, gill cover, and insertion of pectoral fin. Distension just below the gill cover which slowly shifts toward the belly area approaching negative extreme.	Variation in the area near pectoral fin and area of the tail approaching caudal fin. Change in the position of the eye, gill cover, caudal peduncle, and insertion of pectoral fin. Change in length from origin to insertion of anal fin. Distension just below the gill cover which slowly shifts toward the belly area approaching negative extreme.
3 10.05%	Change in the position of the eye, gill cover, posteriormost part of the neurocranium. Change in the length from the origin to insertion of anal fin; origin of anal fin to insertion of pelvic fin; and from origin to insertion of dorsal fin. Change in position of caudal peduncle.	Change in the position of the eye, gill cover, posteriormost part of the neurocranium. Change in the length from the origin to insertion of anal fin and origin of anal fin to insertion of pelvic fin.
4 7.58%	Change in the length from origin to insertion of dorsal fin; from origin to insertion of anal fin; and from origin of anal fin to insertion of pelvic fin.	Change in the length from origin to insertion of dorsal fin; from origin to insertion of anal fin; and from origin of anal fin to insertion of pelvic fin. Change in position of pectoral fin and gill cover.
5 5.47%	Change in the length from the origin to insertion of dorsal fin and from origin to insertion of anal fin. Change in position of caudal peduncle.	Change in the length from the origin to insertion of dorsal fin and from origin to insertion of anal fin. Change in position of caudal peduncle.

To summarize, the main variations that occur in these three populations of *S. fimbriata* are in the curvature of the body of which the Butuan population got the greatest variation; distension in the mid-section of the body near the belly part with the population from Dipolog having the greatest variation; changes in length of dorsal fin, anal fin, and pelvic fin wherein the three populations got almost the same variation; change in position of the eye, gill cover, and most posterior aspect of the neurocranium where the Butuan City population got the least percent variance.

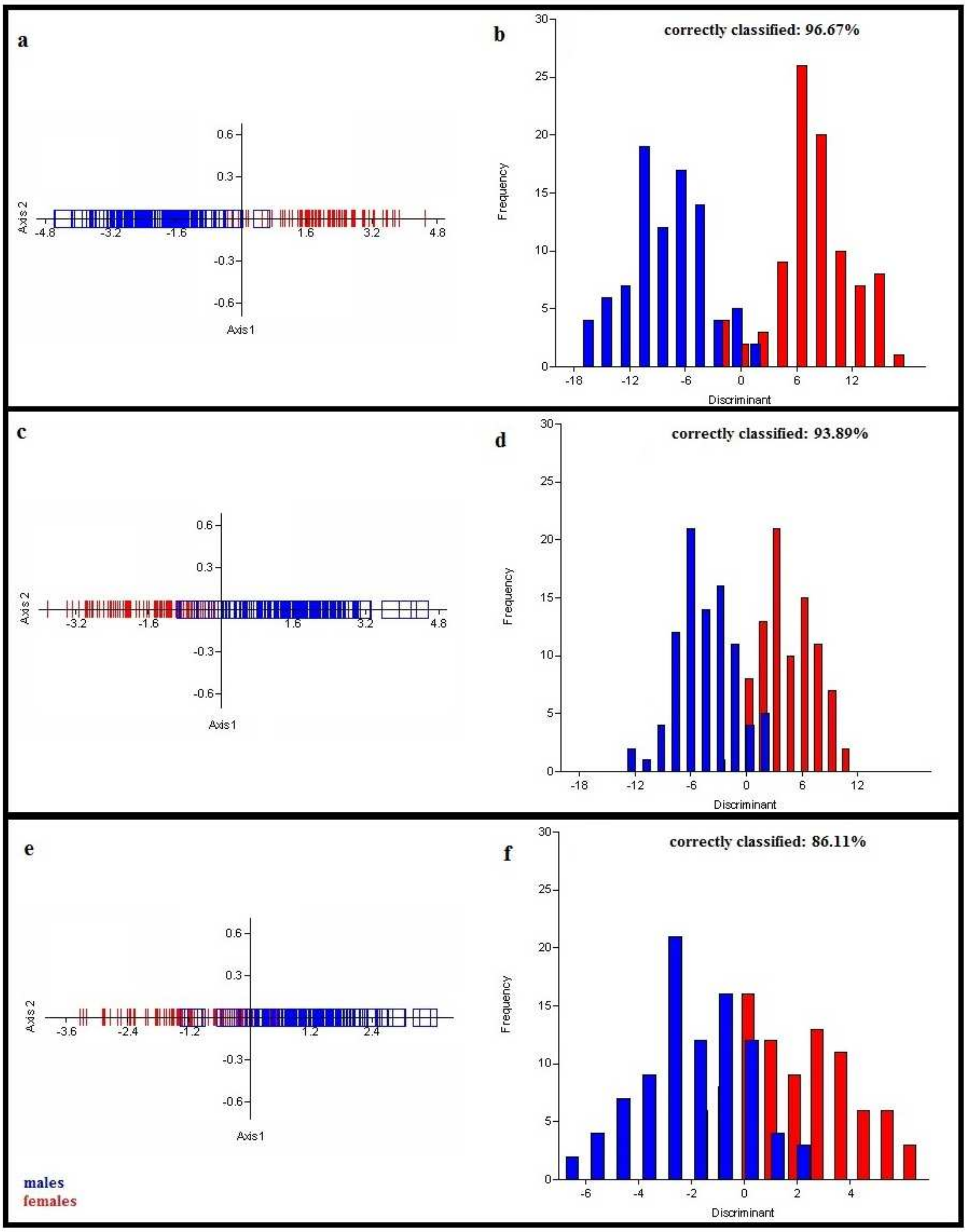

Fig. 4. Canonical VariateAnalysis and Discriminant Function Analysis plots of the relative scores of *S. fimbriata*populations.*(CVA) (a, c, e); (DFA) (b, d, f); Butuan Bay (a,b), Dipolog Bay (c,d),Pagadian Bay (e,f)*

To further emphasize the comparison between the difference of the body shapes between both sexes from each population, statistical tools such as Multivariate Analysis of Variance (MANOVA), Canonical Variate Analysis

(CVA), and Discriminant Function Analysis (DFA) were done. Tables 2 and 3 contain the results from MANOVA and DFA for each of the population respectively.

To show whether there are significant differences in the body shapes of males and females for each of the population, CVA plots and DFA plots were generated (see Figure 4 a, c, and e). Figures 4 a, c, and e show much of the variation between the two sexes and account for nearly 100% of the variance within each of the populations while Figures 4 b, d, and f show the DFA plots of the pooled scores of both males and females of *S. fimbriata* from each population. The DFA plots further emphasizes the difference between the two sexes showing a minimal overlap of some of their morphological characteristics.

Table 2. Summary of the MANOVA results for *S. fimbriata*in the three different populations

	Butuan	Dipolog	Pagadian
Wilks' lambda	0.1825	0.2899	0.4651
Pillai trace	0.8195	0.7106	0.5349
P-Values	3.512E-37; 1.651E-37	8.021E-24; 7.057E-24	3.493E-11; 3.476E-11
Eigenvalue1	4.467	2.446	1.15
Eigenvalue2	0.002477	0.0008075	7.37E-05

Table 3. Summary of the DFA results for *S.fimbriata* in the three different populations

	Butuan	Dipolog	Pagadian
P-Value	3.41E-36	8.926E-24	1.893E-10
Correctly classified (%)	96.67%	93.89%	86.11%

To see the variations existing within sexes between populations, pooled relative warps and boxplots were generated. Figure 5 shows the summary of relative warps with the corresponding variance between populations of *S. fimbriata* [females (a), and males (b)]. The figure shows that in general, the pooled female population exhibit lesser variation in terms of the curvature of the body as well as lesser variation in the compression/decompression of the mid-section of the body and lesser variation in the change in the snout region compared to the male population. The females however, show much variation in the change of length of the dorsal fin while the males show much variation in the change of length from the insertion of pelvic fin to origin of anal fin.

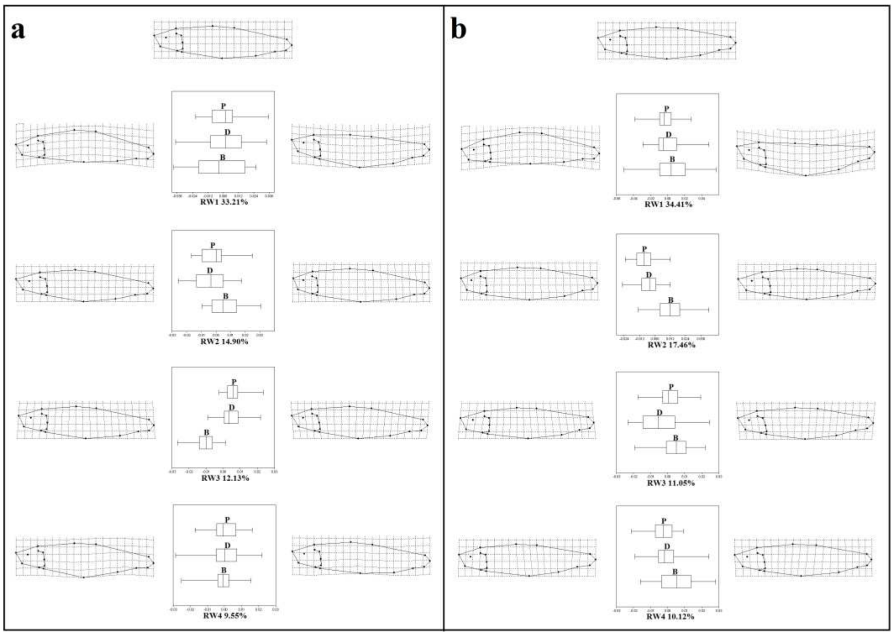

Fig. 5. Summary of landmark based geometric morphometric analysis showing the boxplot and variation of the body shapes between populations of *S. fimbriata*as explained by each of the significant relative warps.*(a) females (b) males*

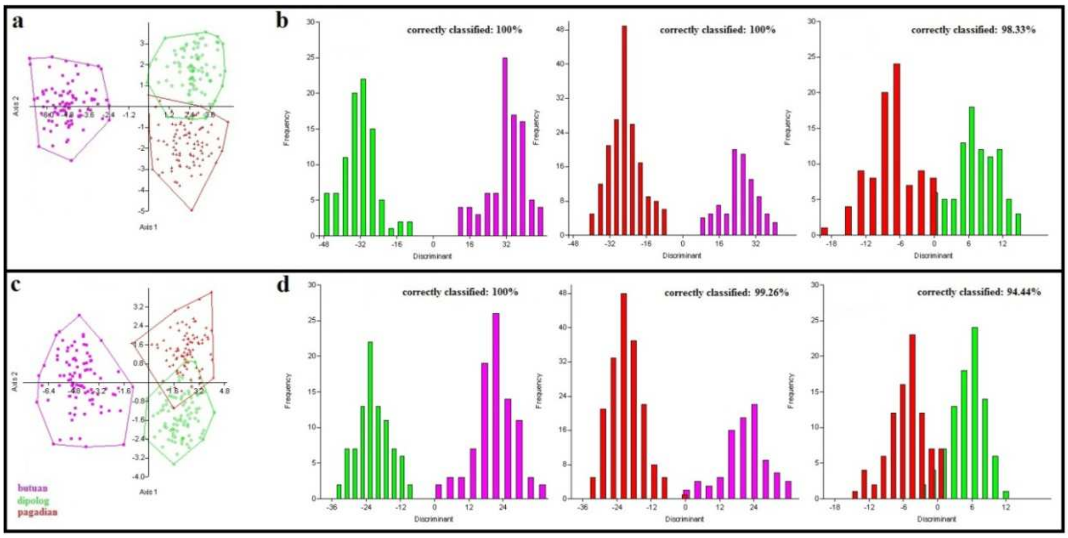

Fig. 6. Canonical Variate Analysis and Discriminant Function Analysis plots of the relative scores of *S.fimbriata* females (a, b) and males (c, d).*(CVA) (a, c), (DFA) (b, d); females (a, b) and males (c, d)*

CVA and DFA plots for within sexes between populations were also done. Figures 6 a and c show the CVAs for each sex and Figures 6 b and d show the DFAs [females (a, b), and males (c, d) respectively. Looking at the CVA plots in each sex, it can be observed that there are significant differences in the morphological attributes existing between the sexes for each population since there is little to no overlap between them, hence each population are separated from each other. The DFA further supports the result obtained in CVA since it shows that there is also minimal overlap (with nearly or 100% correct classification) of the morphological attributes between populations. Tables 4 and 5 contain the results for the MANOVA and DFA between the three populations respectively.

Table 4. Summary of the MANOVA results for *S.fimbriata* females and males between the three populations

	Females	Males
Wilks' lambda	0.02449	0.04037
Pillai trace	1.608	1.47
P-Values	2.875E-146; 7.016E-125	6.412E-122; 7.973E-96
Eigenvalue1	11.85	9.846
Eigenvalue2	2.176	1.284

Table 5. Summary of the DFA results for *S.fimbriata* females and males between the three populations

	Females		Males	
	P-Value	Correctly Classified (%)	*P*-Value	Correctly Classified (%)
ButuanVsDipolog	1.047E-72	100%	5.85E-61	100%
ButuanVsPagadian	2.462E-108	100%	5.048E-100	99.26%
DipologVsPagadian	5.188E-34	98.33%	7.528E-27	94.44%

The MANOVA results obtained from comparing the females and males from each population justifies that there are differences existing between the two sexes, thus, sexual dimorphism has been detected and is existing in the three populations of *S. fimbriata*. Wilks' lambda and Pillai trace emphasize this finding. DFA and CVA are tools that test whether groups or populations can be well separated from each other or blend into each other into a continuum [22]. Looking at the CVA and DFA plots, it can be seen that the females and males overlap at around zero showing minimal overlap allowing separation of the two sexes. Thus, it suggests that there are differences between the two sexes which can be attributed to sexual dimorphism.

Sexual dimorphism is an ubiquitous phenomenon in animal taxa. The three main adaptive mechanisms favouring the evolution of sexual dimorphism according to Hedrick and Temeles[23] are: sexual selection, dimorphic niches, and food competition. Sexual selection typically acts on males, e.g., when females show assortative mating or when mate competition enforces selection on certain male traits. The dimorphic niche hypothesis however suggests selection acting mainly on females due to reproductive constraints [23]. Additionally, ecological selection acting differently on both sexes can influence sexual dimorphism by favouring both dimorphic niches and as a consequence, dimorphic trophic structures [23]. Several studies show that 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]. A few studies also showed sexual dimorphism that has been noted in dorsal and anal fin being pointed in mature males and rounder in females in *Sarotherodongalilaeus* (Linnaeus) and *Oreochromisaureus* (Steindachner) [28], pelvic fins reaching or passing the anus in males but not in females in *Tilapia zillii* (Gervais), *S. galilaeus* and *O. aureus*, [29], a thicker and continuous dorsal fin in mature males and notched dorsal fin in females of *O. aureus*[30], and a thicker lip in upper jaw in mature males of *O. mossambicus*[31]. Such studies show that males and females don't only differ in terms of their reproductive organs but also in external structures that are not directly linked or related to reproduction [24, 32]. Another study revealed that environmental parameters such as salinity can influence fish shape—significant differences in sea bass shape were detected after acclimation to freshwater [33]. Many animals, especially the males, display extravagant characteristics that are used as cues in both female mate choice and male to male competition [24, 34]. In choosing a mate, females would of course prefer males with traits that are honest indicators of quality that are passed on to their offspring [35, 36]. These traits may also indicate social status and resource-holding potential in intrasexual communication [37], demonstrating dominance and/or fighting ability, thereby preventing or reducing the costs of combats with a predictable outcome [38-40]. In the present study, it has been observed that the variations existing in these populations *S. fimbriata* are mainly on the curvature of the body, compression/decompression in the mid-section of the body, change in the dorsal fin length, change in caudal peduncle, and change in the snout region. Thus, it could be that the possible causes of these changes in the body shape of *S. fimbriata* could be attributed to one or few of the factors mentioned above.

The pooled data from the three populations according to the CVA and DFA plots (see Figure 6) indicate that there is a clear difference between the three populations of *S. fimbriata*. This is further supported by the results from the MANOVA exemplified by the Wilks' lambda, Pillai trace, and the P-Values (Table 4 and Table 5). This result may suggest that geographic separation could be a contributing factor to the population's distinction from each other since there is little to no interaction/intermingling and/or migration between these populations [41]. Isolation also permits populations to be subjected to varying selection pressures, one of the preconditions for allopatric speciation. Such isolated populations may become morphologically and genetically differentiated through adaptive or non-adaptive processes [42] eventually leading to formation of distinct gene pools. Hence, the ability of fish populations or stocks to adapt and evolve as separate biological entities is limited by the exchange of genes among populations. Isolation thereby permits notable morphological, meristic and genetic differentiation among stocks within a species, which may serve as a basis for proper management of stocks [41]. A study of Liza abu from the rivers Orontes, Euphrates, and Tigris demonstrated that there were clear distinctions in the morphology between these populations of fish [41]. The same finding was observed in the three populations of *Engraulisencrasicolus* L. from the Black, Aegean, and Northeastern Mediterranean Seas [43]. The distinction between populations observed in *S. fimbriata* in the present study could be attributed to the population's response to their present environment and thus to the present selection pressures existing in each geographical location they are in. One example of selection pressure that could have contributed to their differentiation is overfishing/overexploitation since *S. fimbriata* is one of those fishes in the Philippines reported to be under heavy fishing pressure along with *S. gibbosa* and *S. lemuru*[44]. Consequently, the phenotypic plasticity of fish thereby allows them to respond and adapt to environmental change by modifying their morphology and behaviour which eventually lead to changes in their morphology, reproduction, or survival that alleviate the effects of such environmental change [45].

CONCLUSION

Geometric morphometric analysis was applied in the description of body shapes of *Sardinellafimbriata* from the bays of Butuan City, Dipolog City, and Pagadian City. Results from the MANOVA, CVA, and DFA indicate that there are significant differences between sexes of *S. fimbriata* in each population as well as significant differences within sexes between populations. Hence, sexual dimorphism was observed to be existing in each population. Geographical isolation also is a great contributing factor to the observed distinction between populations of *S. fimbriata* since isolation permits little to no interaction/intermingling between populations causing limitations in the exchange of genes. Additionally, it could also be emphasized that such changes resulted from the response/adaptation developed by each population to their environment or to different selection pressures like overfishing/overexploitaion present in their respective geographical location. Overall, geometric morphometric once again proved its ability to distinguish variations that exist within and among populations. However, knowledge about the genetics of these morphological variations would give this study a more solid ground since knowledge of both phenotypic and genetic aspects are equally important in studying the diversity of an organism especially when it comes to their proper management.

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