Describing the body shape of three populations of Guppy (*Poecilia reticulata*) collected from three rivers in Mindanao Island, Philippines

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Abstract. This study was conducted to describe the body shape variations in *Poecilia reticulata* from three selected rivers in Mindanao Island, Philippines. Landmark-based geometric morphometrics were utilized to analyze the patterns of body shape variations within and between populations of *P. reticulata.* 20 landmarks were selected and digitized on the left side of 90 males and 80 females adult fish. Relative warp analysis was conducted on Procrustes-fitted landmarks and the generated relative warp scores were used as variables for multivariate statistical analysis of variations within, between and among sexes and populations. Results showed sexual dimorphism in body shapes within populations of *P. reticulata*. Females showed downward bent body shapes, while the males showed upward bent, except for fish collected from Tubod, Lanao del Norte, where body shapes between sexes are in the opposite. Variations in body shapes between populations were also observed in the head, midsection of the body, caudal peduncle and insertion of the anal and dorsal fins. It is argued that the morphological variations observed between populations could be attributed to differences in environmental conditions in the selected rivers.

Key Words: procrustes, landmarks, relative warps, geometric morphometrics, canonical variance analysis.

Introduction. Guppies, *Poecilia reticulata* (Peters 1860) commonly known as "million fish", or "rainbow fish" are small benthopelagic, live-bearing fish, that are occupying a wide range of habitats, such as estuaries, lakes, ponds, ditches and canals (Page & Burr 1991). They are primarily fish of shallow waters that tend to be more abundant in smaller streams than in large, deep or fast flowing rivers (Magurran & Philip 2001). As omnivorous individuals, they feed mainly on small insects, zooplankton, algae and detritus. Their broad tolerance to wide a range of salinity (Chervinski 1984), temperature (Gibson 1954; Arai et al 2011) and low oxygen levels (Kramer & Mehegan 1981; Weber & Kramer 1983) make it one of the few species present in mostly all types of freshwater habitats.

As an introduced neotropical species from Northwestern South America (Bisazza 1993) to tropical and sub-tropical countries, it is regarded as a biological agent for the control of vector (mosquito) populations (Stockwell & Henkanaththegedara 2011). In some areas, it is viewed to be beneficial as a control agent (Juliano et al 1989) but in other areas, it is reported to have a minimal effect on mosquito populations (Castleberry & Cech 1990). The accidental release of guppies from both hobbyists and rearing facilities is the most likely cause of many introductions of small exotic ornamental fish into non-native areas (Wellcome 1988) and they are now widely established throughout temperate and tropical freshwater systems worldwide. Its widespread has been implicated in the decline of some species in its introduced range by predation (Deacon et al 1964; Sigler & Sigler 1987; Courteny et al 1988) and as a disease agent, since it is a known carrier of trematode parasites, which may affect native fish populations (Leberg & Vrijenhoek 1984).

This species represents one of the best vertebrate models for the study of how phenotypic variation within a population is linked to the adaptation to specific environmental conditions. Guppies possess morphological characteristics that allow them to live under different environmental conditions (Robinson & Wilson 1994). Some authors reported correlations between body shape, diet, habitat and predation risk in guppies, where differences in morphology were used to explain differences in the exploitation of trophic and spatial resources (Robinson & Wilson 1994; Dowdall et al 2012; Solis et al 2014). Since its introduction to the Philippines in 1905 as a biological agent for the control of vector (mosquito) populations, their abundance and wide distribution in different water systems can be attributed to its full adaptation that could be reflected in their body shape. Since many fish are distributed over a wide range of habitats, thus experiencing a wide range of environmental conditions, their adaptations to different selection regimes among alternative environments may require morphological traits that help them survive in a specific habitat and make them efficient and successful competitors (Bugas et al 2013). Studies have shown that the ability of fish to adapt successfully to all kinds of environmental conditions has long been regarded as a requisite for survival (Fuimann & Batty 1997); thus, this study was conducted. We investigated variations in morphological characters and whether there were differences in populations based on the differences in freshwater habitats where they were observed.

Material and Method. The present study was carried out from June 2015 to December 2015. *P. reticulata* were collected from three river ecosystems in Mindanao, Philippines (Figure 1), namely: Tambulig, Zamboanga del Sur (804’23”N; 123032’39”E), Alegria, Surigao del Norte (9029’42”N; 125034’47”E) and Tubod, Iligan City (8013’15”N; 124013’29”E). Specimens of *P. reticulata* were collected using a hand net and males were sorted from females through the identification of observable physical attributes, like the presence of the gonopodium. There were 30 males and 30 females obtained from Tambulig, Zamboanga del Sur and Tubod, Iligan City and 30 males and 20 females in Alegria, Surigao del Norte. The samples were immediately kept in a separate styrofoam box with ice for processing and detailed analysis.

Figure 1. The geographic location of the study sites in Mindanao, Philippines.

Geometric morphometric analysis of shape variations. The fish specimens were photographed from the left side of the body using a DSLR Canon camera, with 105 mm lens, while lying on a straight horizontal position on a white background. The fins were stretched out and pinned. The obtained images were then subjected to landmark-based geometric morphometric analysis (GM).

GM analysis was used to quantify morphological differences within and among populations of *P. reticulata*. A total of 20 landmarks (20 x and 20 y coordinates) were selected and digitized on the left side of each specimen, using the tpsDig2 software version 2.16. These 20 landmarks are as follows: (1) anterior tip of the snout, (2) dorsal occiput, (3) dorsal outline halfway between the dorsal occiput and anterior insertion of dorsal fin, (4) anterior insertion of dorsal fin, (5) posterior insertion of dorsal fin, (6) dorsal outline halfway between posterior insertion of dorsal fin and dorsal insertion of caudal fin, (7) dorsal insertion of caudal fin, (8) posterior body extremity, (9) ventral insertion of caudal fin, (10) ventral outline halfway between the ventral insertion of caudal fin and the posterior insertion of anal fin, (11) posterior insertion of caudal fin, (12) anterior insertion of anal fin, (13) ventral outline halfway between the anterior insertion of anal fin and the insertion of the operculum on the lateral profile, (14) lower insertion of pectoral fin, (15) upper insertion of pectoral fin, (16) superior insertion of operculum, (17) point of maximum extension of operculum on the lateral profile, (18) insertion of operculum on the lateral profile, (19) anterior margin of the eye, (20) posterior margin of the eye (Figure 2). Landmarks 3, 6, 10 and 13 were treated as sliding semilandmarks.

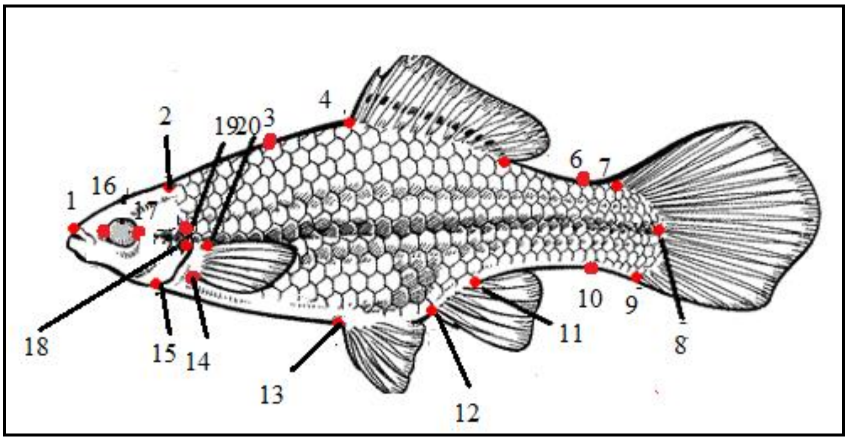

Figure 2. Morphometric landmark locations for *Poecilia reticulata*.

The TPS software was used to digitize the identified landmarks. The x and y coordinates (using TPSdig prog) were collected and were superimposed by Generalized Procrustes Analysis (GPA), using the TpsRelW software version 1.49 to preserve all information about the shape. The data not related to shape (position and orientation) were removed (Mitteroecker & Gunz 2009; Haas et al 2010; Hossain 2010). The GPA produces the general shape used as a reference to all subsequent analyses of variations in shapes within, between and among sexes and populations. The variation was shown as a deformation of the grids.

The results gathered from the relative warp analysis include histograms and box-and-whiskers-plots generated using the PAST software (Hammer et al 2001). To compare within, between and among sexes and populations, the relative warp scores were subjected to Canonical Variance Analysis (CVA) and Discriminant Function Analysis (DFA) using the same software. The generated histograms and box plots were used to visualize data distribution over variable ranges.

Results and Discussion. Figure 3 illustrates the pattern of the body shape variation within the population of *P. reticula*ta from the three rivers. Boxplots of the relative warp (RW) scores, mean shape and morphological differences are graphically shown in Figure 4. The descriptions of the shapes between sexes within populations are summarized in Table 1.

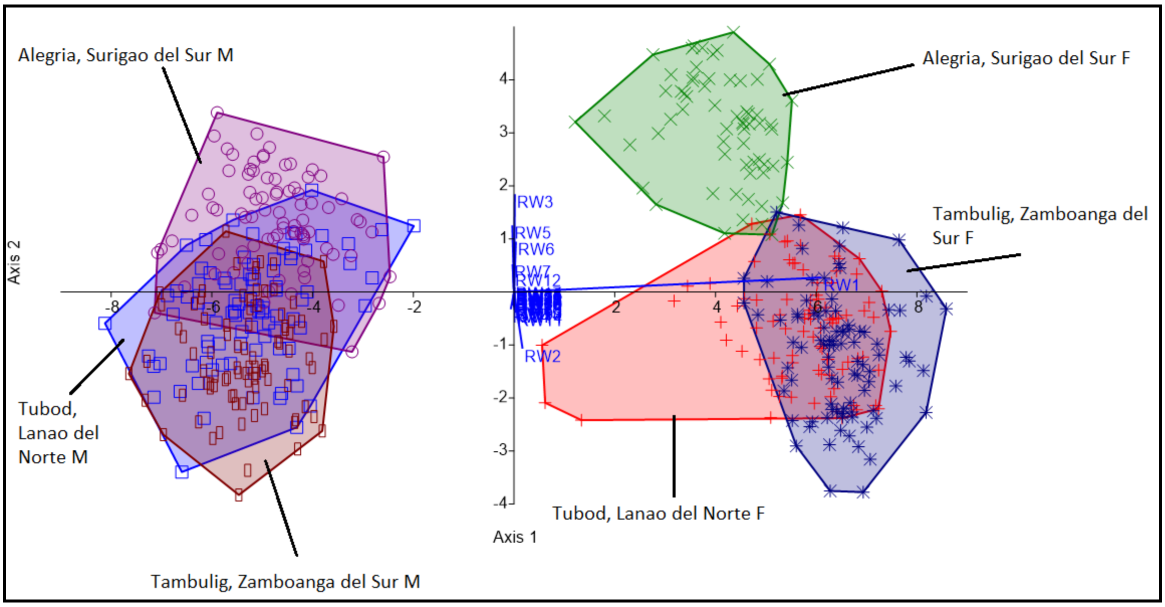

Figure 3. Canonical variance analysis of relative warp scores showing the distribution of individual guppies.

It can be seen from the results that sexual dimorphism was observed within populations. For the Tambulig population, the first relative warp extracted from the matrix of the partial warp scores accounted for 72.39% of the total nonaffine shape variation, while the 2nd relative warp only explained 13.76% of the total difference. Shape changes characterized by the first relative warp show an upward arching of the body for males, while a downward bent body was observed in the female body curvature. Males were also observed by an upturned mouth and upward position of the eyes when compared to the downward eyes and sub-terminal mouth orientation in females. The second relative warp is characterized by shape differences in the body height, head size and caudal peduncle shape. Males exhibit a more robust body, a smaller head, a shorter and a deeper caudal region compared with females.

For Tubod, Lanao del Norte population, sexual dimorphism was also observed. The first relative warp score (RW1) explains 69.04% of the total variation found, where females showed a more pronounced downward bending of the body than males. The RW2 result accounts for 14.06% of body shape variation that is mainly concentrated in the body depth. Males demonstrate a deeper body width than females. The size of the head and eyes are reduced in males and difference in the caudal peduncle region is seen, with males showing a more in-depth and shorter caudal peduncle compared with females. Furthermore, males also exhibit a lengthier base of the dorsal fin and anal fin than females.

The population of *P. reticulata* from Alegria, Surigao del Norte shows differences in the body shape for both sexes of *P. reticulata*. The first relative warp (68.56%) described variation in the form of the body curvature, as well as in the orientation of the mouth, position of the eyes and the caudal peduncle. Both sexes exhibit body bending, which is greater in males than in females. A superior mouth, an upward position of the eyes and a long slender caudal peduncle are observed in males, while females exhibit a terminal mouth, ventrally placed eyes and a shorter broader caudal region. The 2nd relative warp (12.77%) is associated with variation in the midsection of the body. The females possess a greater body height as compared with the intermediate body depth of males. Females also exhibit a reduced head, smaller eyes, a deeper shorter caudal peduncle, and a posteriorly positioned anal fin and dorsal fin compared to males. In addition, the anal fin base length is longer in females than in males.

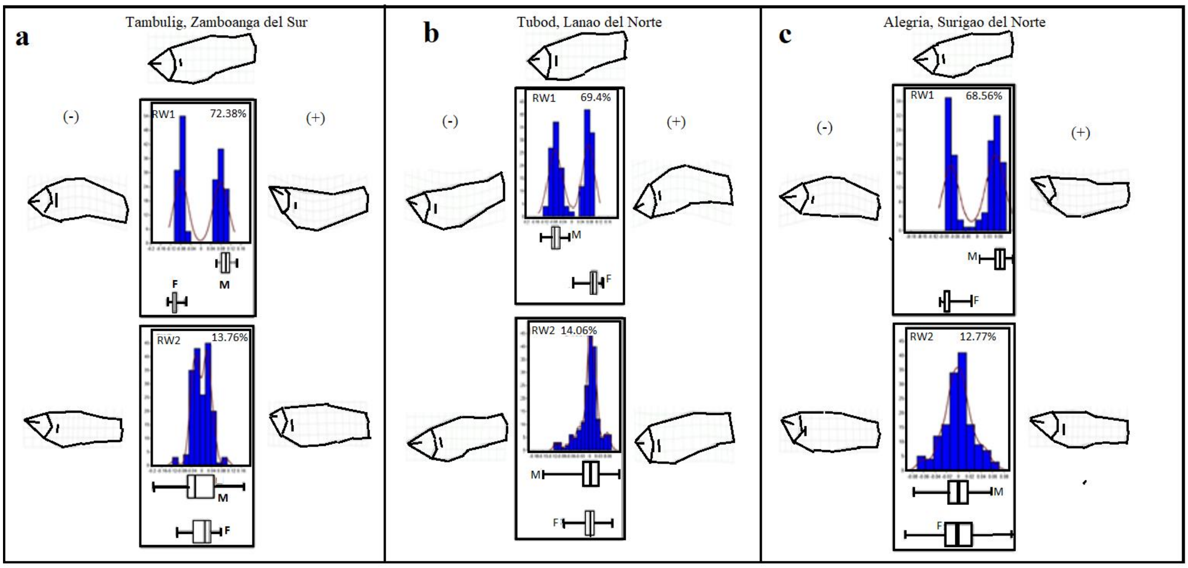

Figure 4. Summary of landmark-based geometric morphometric analysis showing the consensus morphology and the variation of body shapes between sexes of *Poecilia reticulata* from the rivers of (a) Tambulig, Zamboanga del Sur, (b) Tubod, Lanao del Norte, (c) Alegria, Surigao del Norte, as explained by each of the significant relative warps.

To compare whether the three populations vary in body shapes, the relative warp scores for both sexes were subjected to Canonical Variate (CVA) and Discriminant Function (DFA) analyses (Table 2). Between populations comparison revealed by the CVA, analysis indicates that the populations vary from each other. Graphical presentation of the CVA analysis (Figure 2) revealed that the body shape of males is relatively different from that of females. Discriminant Function Analysis (DFA) providing a matrix to show the classification of males and females into the correct group revealed 85.56-95% correct classification (Table 3). It can be seen from the results that less than 10% of individuals are misclassified to other groups. The results, however, clearly show population differentiation as the discrimination is more than 70% of the expected acceptability.

The differences in the morphological characteristics studied within and between populations of *P. reticulata* could be a consequence of phenotypic plasticity among many freshwater fish species (Barazona et al 2015; Cagata et al 2010; Dorado et al 2012; Ganzon & Demayo 2017; Hermita et al 2013; Kitche-Arreglado 2013; Luceno & Demayo 2017; Luceno et al 2018; Matondo et al 2012; Nacua et al 2010; Nacua et al 2012; Pattuinan & Demayo 2017; Pattuinan & Demayo 2018; Perpetua et al 2013; Portillo et al 2017). Such morphological variations are considered to be an essential adaptive strategy to survive a very complex environment (Herath et al 2014; Robinson & William 1994). It is believed that different environmental pressures, such as water depth, water flow, prey abundance, predation, substrates type and anthropogenic practices acting in the habitat cause morphological variations in the population.

The morphological differences observed in the head region, the midsection of the body, caudal peduncle and the insertion of the anal fin and dorsal fin can be argued to variations in the feeding behavior (Anderson et al 2005; Cullen et al 2007) and foraging performance of fish (Watson & Balon 1984). Males from Tambulig, Zamboanga del Sur and Tubod, Lanao del Norte have a reduced size of the head, smaller eyes, that are oriented upward and an oblique or superior mouth compared with the females. The males in Alegria Surigao del Norte have a more massive head, larger eyes and a superior mouth compared with females. It is argued that the size of the head is directly related to food consumption (Winemiller 1991) since more prominent head regions maximize buccal volume and suction velocity (Caldeccut & Adams 1998).

Table 1

Description of body shape variation of *Poecilia reticulata* based on the significant results of the relative warp analysis

Relative warp score	*Female*	*Male*
	Tambulig, Zamboanga del Sur	
1 72.39%	Downward bending curvature of the body, head shape and distance of operculum to the snout.	Upward bending curvature of the body, head shape and the orientation and position of the mouth.
2 13.76%	Changes in the midsection of the body, full body depth, variations in the head shape along with the changes in the size of the eyes and caudal peduncle region.	Observed changes in body depth, a more streamlined body, an elongated head, and a slender caudal region.
	Tubod, Lanao del Norte	
1 69.04%	Variation in the curvature of the body slightly bent in a downward fashion, as it reaches towards the mean — a change in the orientation and position of the eyes and mouth.	Variation in the curvature of the body, bending of the body upward, changes in the orientation and position of the eyes and mouth.
2 14.06%	Some individuals show variation in the midsection of the body showing a more pronounced full body depth with a head that is slightly reduced. Change in the size of the eyes, the position of the gill cover and a broader, wider caudal region.	Variation in the body depth, pointed snout and a narrower, elongated head in many individuals. Change in length from origin to insertion of the dorsal fin and from the origin to insertion of the anal fin. Change in the position of the gill cover and a longer caudal peduncle.
	Alegria, Surigao del Norte	
1 68.56%	Variation in body curvature showing an upward bending of the body. Observable changes in the orientation and position of the eyes and mouth and the location of the pectoral fin.	Variation in the curvature of the body showing an upward bending of the body, changes in the head size, gill cover and the position of the pectoral fin.
2 12.77%	Females have a full body shape in the midsection, present change in head size, the position of the eyes and a more in-depth, shorter caudal region.	Slender variation in the midsection area of the body, slightly compressed abdomen, changes in the head shape, size of the eyes and a long, slender caudal peduncle.

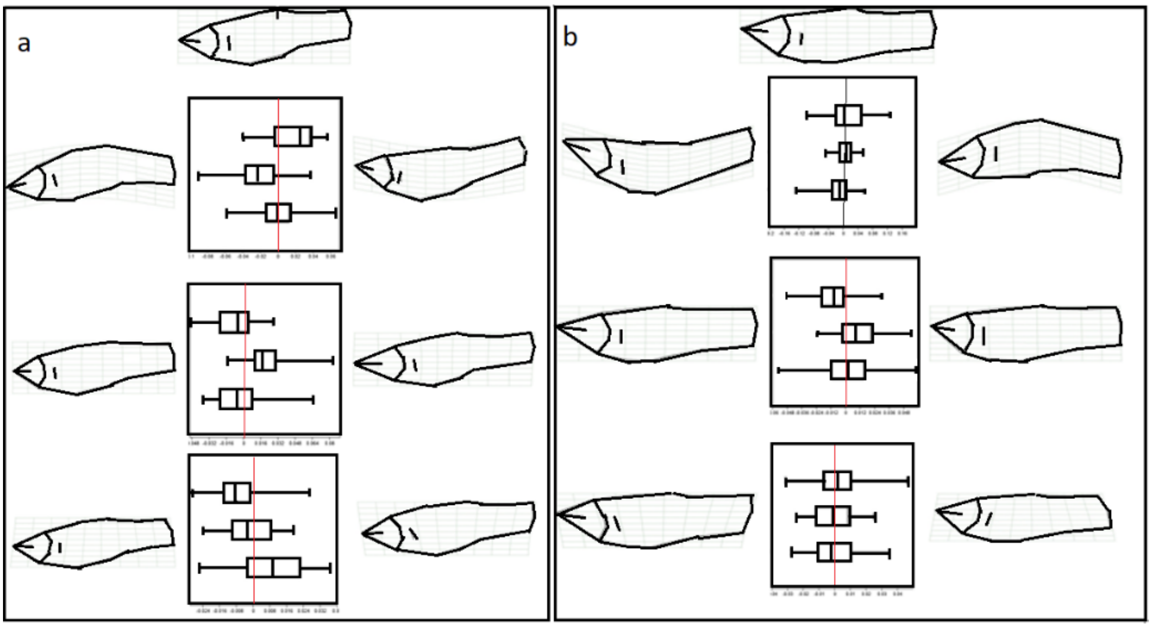

Figure 5. Summary of the geometric morphometrics showing consensus morphology and the variation in the body shape between *Poecilia reticulata* females (a) and males (b).

The results of the study also showed that the sizes of the eyes differ between and among populations. Since the primary source of sensory information in some fish is vision (Pitcher 1993), the presence of large eyes could be an adaptation to low light intensity in the water (Schliewen et al2001). The Alegria river, for example, is characterized by shallow depth, fast flowing waters and a muddy substrate making the water more turbid. Thus, it can be assumed that a means to cope with the turbidity is to increase the eye size to capture the decreased incoming light (van der Meer & Anker 1983). Having large eyes would significantly improve their feeding abilities, especially in detecting prey. In addition to the eye size, the eye position also varies, with males having an upward eye position. This position is presumably involved in an upward pointing visual field. The lower area of the eyes may enhance the detection of a predator in the environment (Langerhans & De Witt 2004).

Table 2

Results of Multivariate Analysis of Variance between the three populations of females and males of *Poecilia reticulata*

	Females	*Males*
Wilks' lambda	0.4617	0.7638
Pillai trace	0.5582	0.25
P-values	5.964E-39; 5.267E-33	2.077E-14; 2.461E-14
Eigenvalue1	1.083	0.2013
Eigenvalue2	0.03972	0.08987

The observed changes in the mouth might reflect differences in selection of food item and direction of feeding (Langerhans et al 2003). An upturned mouth or superior mouth exhibited by males among the studied population is a trait common to surface feeding fish (Winemiller 1991), while a terminal mouth and sub-terminal mouth in females are characteristics of midwater and benthic feeders, respectively. Lawal et al (2012) reported that *P. reticulata* is an opportunistic benthopelagic omnivore, whose feeding habits are determined by the local abundance and availability of prey in the environment. However, data on the stomach contents of the species are still needed to identify whether the observed changes in the mouth and head between sexes and populations could be attributed mainly to differences in the kind and availability of the prey in the complex habitat. It can also be argued that differences in spatial distribution, physical environment and use of the various food resources (Croft et al 2003) by the different populations may also indicate the prevalence of habitat segregation in populations of *P. reticulata*. Furthermore, studies have also shown that females reside mostly in the deeper portions of the water body to avoid male sexual harassment (Darden & Croft 2008).

Table 3

Results of Discriminant Function Analysis (DFA) between the three populations of females and males of*Poecilia reticulata*

	Tubod, Lanao del Norte F	*Tubod, Lanao del Norte M*	*Alegria, Surigao del Sur F*	*Alegria, Surigao del Sur M*	*Tambulig, Zamboanga del Sur F*	*Tambulig, Zamboanga del Sur M*	*Total*
Tubod, Lanao del Norte F	85(94.44%)	0	0	0	5(5.56%)		90
Tubod, Lanao del Norte M	0	79 (87.78%)	0	6 (6.67%)	0	5 (5.56%)	90
Alegria, Surigao del Sur F	3 (4.76)	0	60 (95.24%)	0	0	0	63
Alegria, Surigao del Sur M	0	5(5.95%)	0	77 (85.56%)	0	2(2.38%)	84
Tambulig, Zamboanga del Sur F	7(7.78%)	0	0	0	83 (92.22%)	0	90
Tambulig, Zamboanga del Sur M	0	5(.56%)	0	4(4.44%)	0	81 (90.0%)	90
(94.87 correctly classified)							

For the differences in body depth and the caudal peduncle, which influence swimming performance (Webb 1984) and foraging strategies (Sharpe et al 2008). Male fish from Tambulig and Tubod Rivers presenteda deeper body depth and a shorter caudal peduncle than the Alegria population. These morphological traits are vital in the maneuverability and burst swimming speed (Schluter et al 2004) in fish and are thus considered necessary in the exploration of the more structurally complex environment of the two rivers. These rivers were observed to have many hiding places, floating vegetation, muddy sediments and other organic matter and thus may have been influential in the selection of fish with deeper body depth and caudal peduncle. A deeper body is also beneficial especially in an environment with predators (Domenici et al 2008), so the variations observed in body shapes could be an adaptive response to evade predators. The placement of the dorsal fin and the anal fin also differs within and among populations of *P. reticulata*. Although the insertion of the dorsal fin and anal fin differ in the three fish populations, these structures serve the same purpose, with the anal fin used to stabilize swimming and dorsal fin to protect the fish from rolling and assist in sudden turns and stops (Lindsay 1988). These differences could have been affected by the hydrodynamics of the habitat. The summary of the differences in body shape between females and males are presented in Figure 5.

It can be summarized from the results of this study that the body shape of the fish and its associated morphological parts, such as fins, caudal peduncle are an obvious adaptation about where and how the fish live. Habitat type, predators and food availability are interacting features that can be argued to have influenced morphological responses in the fish populations. Studies have shown that fish occupying lotic habitats possess morphological features that enhance swimming performance, such as a streamlined bodies, shallow/narrow caudal peduncle and a higher aspect ratio of caudal fins, while fishes inhabiting lentic habitats have deepened body shape, larger caudal peduncle, smaller head and lower aspect ratio of caudal fins that enhance unsteady swimming (Langerhans 2008; Langerhans & Reznick 2009). In response to predators, a deeper body, longer dorsal spines, larger caudal peduncles and a smaller cranial region are the central adaptations to evade predators and increase chances of survival (Abrahams 2006). Studies on 16 different species have shown a smaller lower anterior region and a broader caudal region in populations at high predation localities or treatments (Langerhans 2010). Likewise, it was shown that variations in head and mouth shapes could appear due to the reflective of differences in selection of food items and the direction of feeding in fishes (Langerhans et al 2003). Information about the morphological characters of fish therefore provide insights about the ecological niches of fish (Winemiller 1991) allowing inferences about its distribution (Watson & Balon 1984), trophic patterns (Hugueny & Pouilly 1999) and predicting its life habitats (Keast & Webb 1996; Karr & James 1975).

Conclusions. The morphological differences within, between and among the three populations of *P. reticulata* using landmark-based geometric morphometric analysis include differences in body curvature, body depth, head size, orbit diameter, mouth orientation, caudal peduncle shape and placement of dorsal and anal fins. These differences could be an adaptive response to the selection pressures upon three geographically distant populations of *P. reticulata*, although it is also likely that phenotypic plasticity plays an essential role in the observed changes, as a main driving force behind the observed variation.

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