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Abstract

Morphological features of three reef fishes with varying larval dispersal strategies: *Acanthochromis polyacanthus*, *Naso lituratus*, and *Scarus quoyi* were assessed using landmark-based geometric morphometrics. Samples were collected from Pujada Bay, Sarangani Bay, and Davao Gulf, spanning a distance of ~300 km. Analysis of the transformed landmarks using multivariate analysis of variance (MANOVA) and pairwise Hotelling's test using Bonferroni showed significant differences in the populations of each reef fish, thus, were phenotypically separable across sites. Our results further revealed that these differentiations result from variation in body shape, mouth, fins, and operculum. Differentiation was expected in *A. polyacathus* as it lacks pelagic larval duration (PLD), implying its limited dispersal potential. Interestingly, similar pattern was observed in both *N. lituratus* and *S. quoyi* even with long PLDs. This suggests that at distances as short as ~100 km, populations of reef fishes may exhibit morphological heterogeneity despite their dispersal potential.

Keywords: landmarks, local adaptation, pelagic larval duration

Introduction

Understanding population structure of reef fishes have been the core of fishery management and conservation biology studies (Thorpe *et al*. 1995). But with the current impending issues of overexploitation (Green *et al*. 2003, Nañola, Aliño & Carpenter 2011) coupled with increased use of unsustainable fishing methods, it is not surprising why fish stocks continue to decrease exponentially. The dilemma was worsened due to unfit management practices that lack information on organism's life-history traits and the physical processes affecting them.

Fortunately, recent advances in scientific tools and methods such as biophysical modeling, morphometrics, and population genetics have not only helped address these concerns but also provide estimates on the spatial scale of population isolation. Barber *et al*. (2000) in their study on ecological connection in the Coral Triangle suggest that differentiation can be expected in distances as short as 300-400km. This estimation, however, may change depending on the dispersal strategy of a reef fish species with respect to the time that its larvae spend in the plankton, the pelagic larval duration (PLD) (Cowen & Sponaugle 2009).

In reef fishes with no pelagic larval duration such as *Acanthochromis polyacanthus* Bleeker, differentiation can be observed even in short distances (Planes *et al*. 2001) as its ability to transport larvae is limited (Thresher 1985). But defining the patterns of dispersal of reef fishes with pelagic larvae, e.g. *Scarus quoyi* Valenciennes (PLD:19-42 days, Ishihara & Tachihara 2011) and *Naso lituratus* Forster (PLD>90 days, Klanten 2003), remains a major challenge because dispersal is driven by multiple complex factors (Palumbi 2003, Mumby 2005). With the potential of long-distance larval transport, local populations are expected to be replenished by larvae derived from elsewhere (Mora 2004) that possess similar morphometric features to its parental sources. However, morphometric features can be very sensitive to changes in the environment (Fryer & Iles 1972), thus, exposure to dynamic reef systems entails developing characteristics which are suitable for underlying physical, chemical and biological stressors in the environment known as local adaptation. This has been shown in studies of morphological differences between and among populations of reef fishes at various spatial scales (Cavalcanti, Monteiro & Lopes 1999, Arreglado *et al*. 2013).

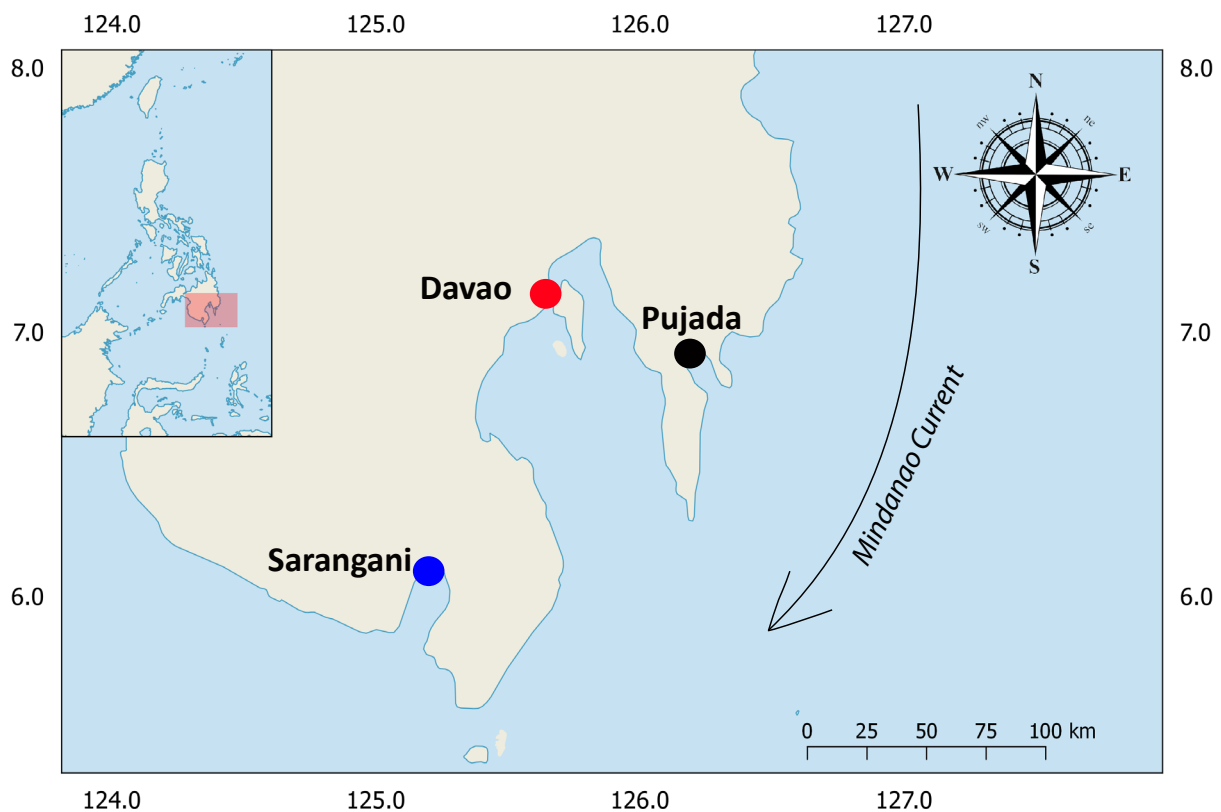The present study was conducted to evaluate

Fig. 1 Map of the Southern Philippine Seas showing the three collection sites, Sarangani Bay (blue circle), Davao Gulf (red) and Pujada Bay (black).

morphological differentiation in the populations of three representative reef fishes, *A. polyacanthus*, *S. quoyi*, and *N. lituratus* in the southern Philippines. Additionally, this study aimed to determine which specific morphological characters contributed to the heterogeneity of these populations.

Materials and Methods

Collection of samples

Approximately 30-60 individuals of *A. polyacanthus*, *S. quoyi* and *N. lituratus* were collected between April 2013 and April 2015 in Pujada Bay, Davao Gulf, and Sarangani Bay (Fig. 1). These sites were chosen for being influenced by a single major current, the Mindanao current, yet provide distinct habitats for reef fishes. Individually, the sites had varying degree of current flow. The order of current flow outside of these areas from slowest to strongest is Pujada, Davao and Sarangani. Further at the site level, the two latter sites had steeper slopes compared with the site in Pujada. In terms of distances among the sites, the longest was around

300 km with which an ecological connection may no longer be possible (Barber *et al*. 2000). Samples from Sarangani and Davao were collected by hired fishers whereas collection in Pujada Bay was made from the market.

Morphometric analyses

Each individual specimen was properly tagged and placed on a measuring board for digital printing using a digital camera (HPd3000 with 21x Optical Zoom) following the protocol introduced by Adams, Rohlf & Slice (2004).

In this study, a landmark-based geometric morphometric analysis was carried out on the resulting images because points were well-defined and homologous from one specimen to the next. The photographs were processed using Thin Plate Spline tpsUtil.exe and tpsDig.exe for the establishment of landmarks (Fig. 2) and to generate its *x* and *y* coordinates. The raw coordinates were transformed and scaled to match using 2D procrustes through Paleontological Statistics (PAST) software, so that values were independent of size.

Under PAST, the transformed morphometric data was applied to canonical variate analysis (CVA) to obtain a scatter plot of specimens along the axes, producing maximal
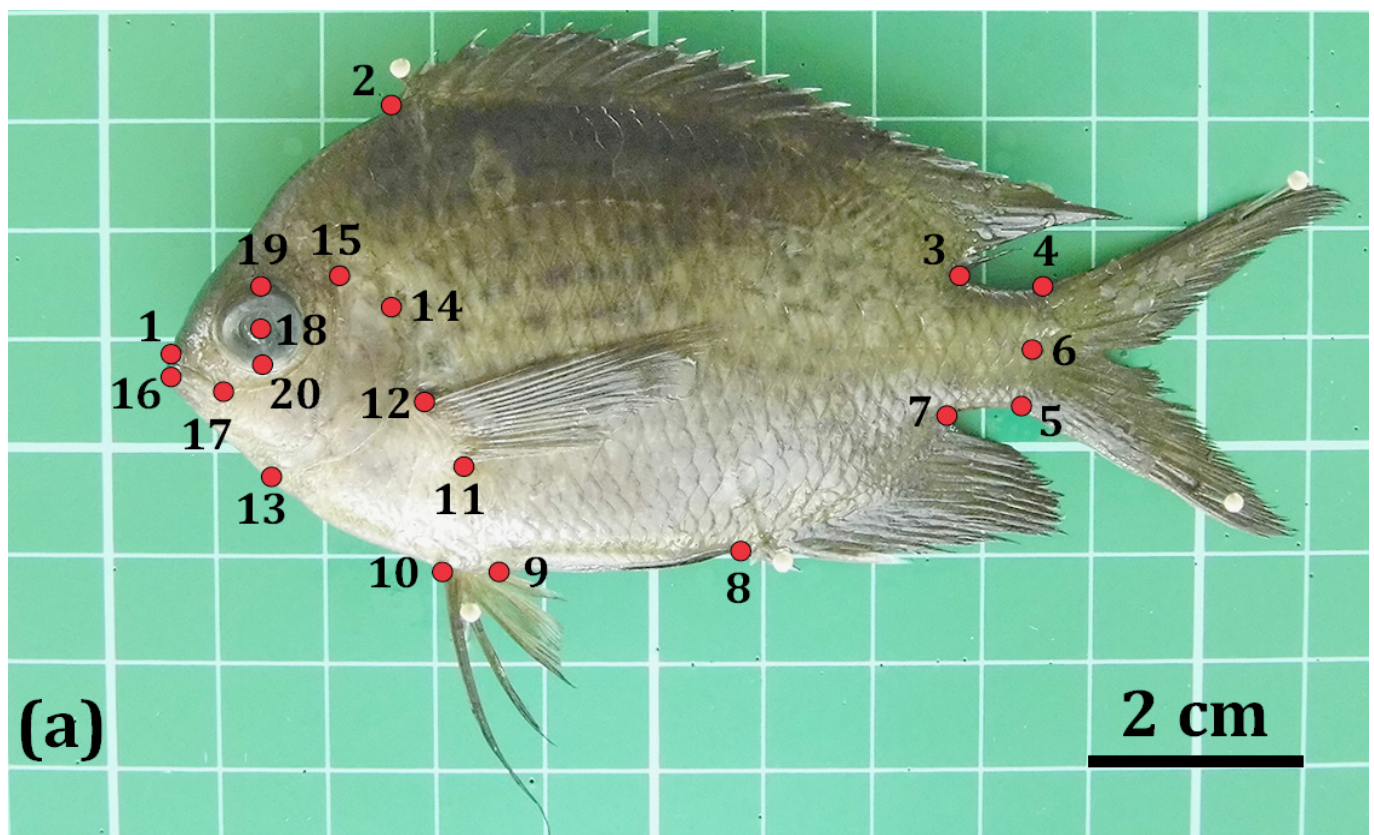

Fig. 2 Digitized landmarks in (a) *Acanthochromis polyacanthus*   [continued to next page]
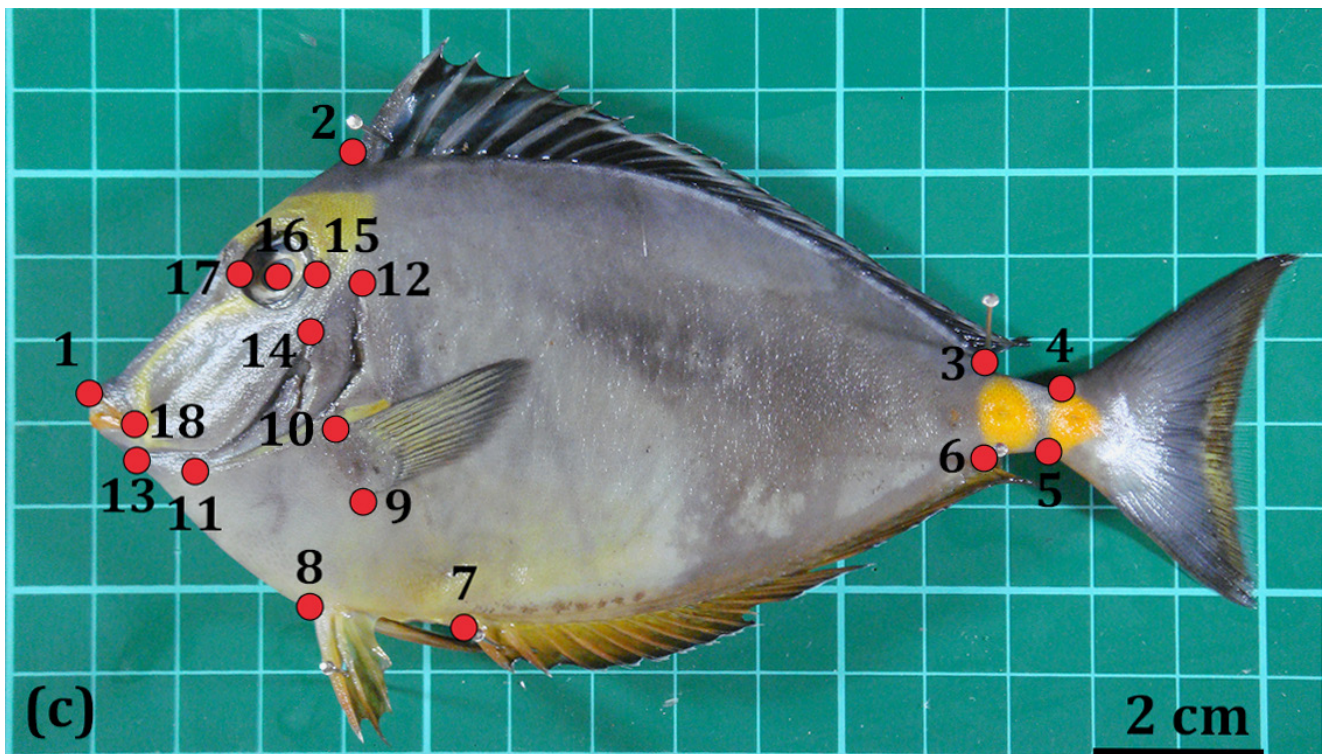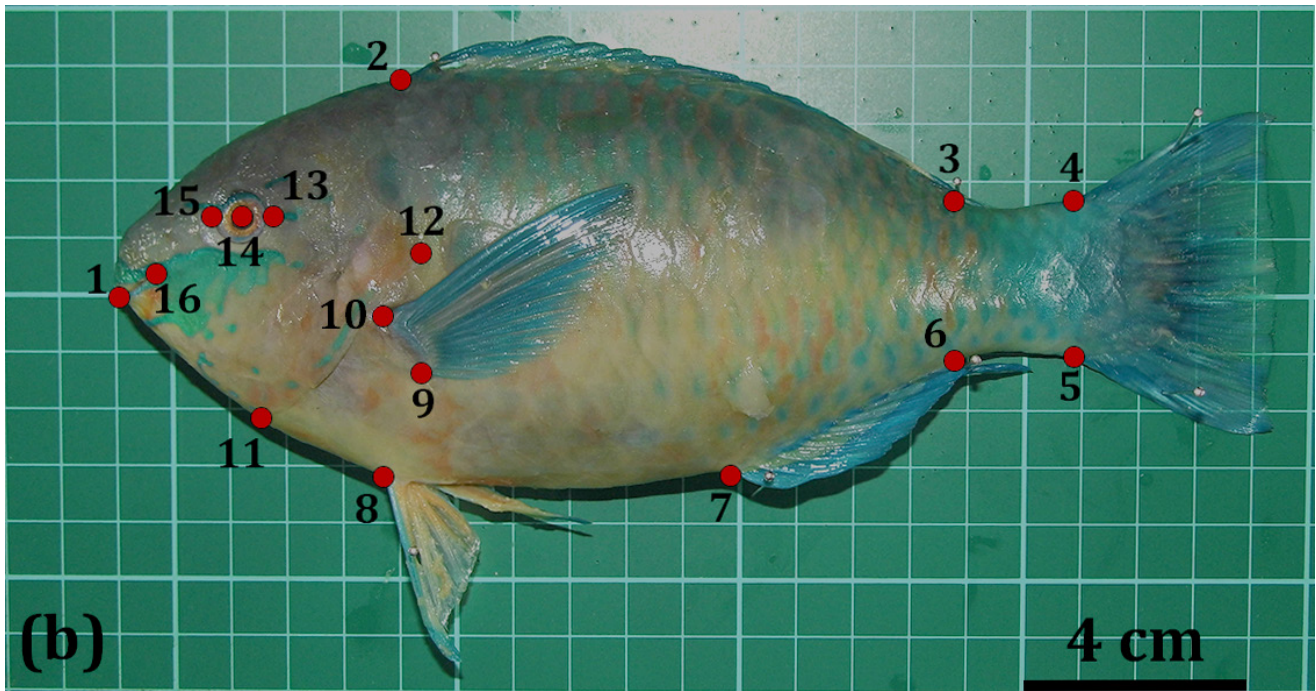
Fig. 2 continued.　Digitized landmarks in (b) *Scarus quoyi* and (c) *Naso lituratus*

separation of all groups at 95% concentration of ellipses. Relative warps were also done to display the direction of shape differences among species. Moreover, relative warps also described shape deformations (i.e. contraction or expansion) of the reference configuration of all the landmarks at different spatial scale.

The significant differences among the investigated populations were initially tested using multivariate analysis of variance or MANOVA (Wilks' lambda and Rao's *F*). The number of constraints or dependent variables was adjusted from zero to four as suggested by Hammer, Harper & Ryan (2001). Those MANOVA results that showed significant differences between all groups were further subjected to pairwise Hotelling's test using Bonferroni (Hammer, Harper & Ryan 2001).

Lastly, the biplot of the principal component analysis (PCA)

was carried out to look for other landmarks that account for the bulk of the variation. These measured landmarks were all set into a central axis that served as the point of similarity for all superimposed landmarks among populations within the same species. A longer line from the central axis implies greater variability in the landmark.

Results

Acanthochromis polyacanthus

Clustering of populations by 95% ellipses showed three distinct groups for *A. polyacanthus* (Fig. 3a). Specifically, Pujada Bay and Davao Gulf specimens were more similar in terms of body shape than to those from Sarangani Bay. Divergence of the Sarangani Bay population was evident along axis 1 characterized by a broader body type (expansion of the belly), a shorter snout (inward displacement) and an upward displacement of dorsal landmarks. The

two remaining groups of *A. polyacanthus* were further differentiated along axis 2 with notable shape differences in the caudal and pelvic fins.

Scarus quoyi

No clear separation was observed in the CVA plot of *S. quoyi* individuals (Fig. 3b). However, weak signals of clustering can be observed in the positive score of axis 1 causing divergence of the Sarangani Bay population from the rest of the groups. Between Davao Gulf and Pujada Bay populations, the former had most individuals with a positive score on axis 2 while the latter were mostly scattered with negative scores. Relative warps of the different populations of *S. quoyi* revealed that in Sarangani, individuals in general have a broader body type (expansion of most body parts), a unique characteristic that was also observed in *A. polyacanthus* of the same site. A prevalent contraction of mouth, pectoral fins and caudal fins partially separated Pujada Bay from Davao Gulf.
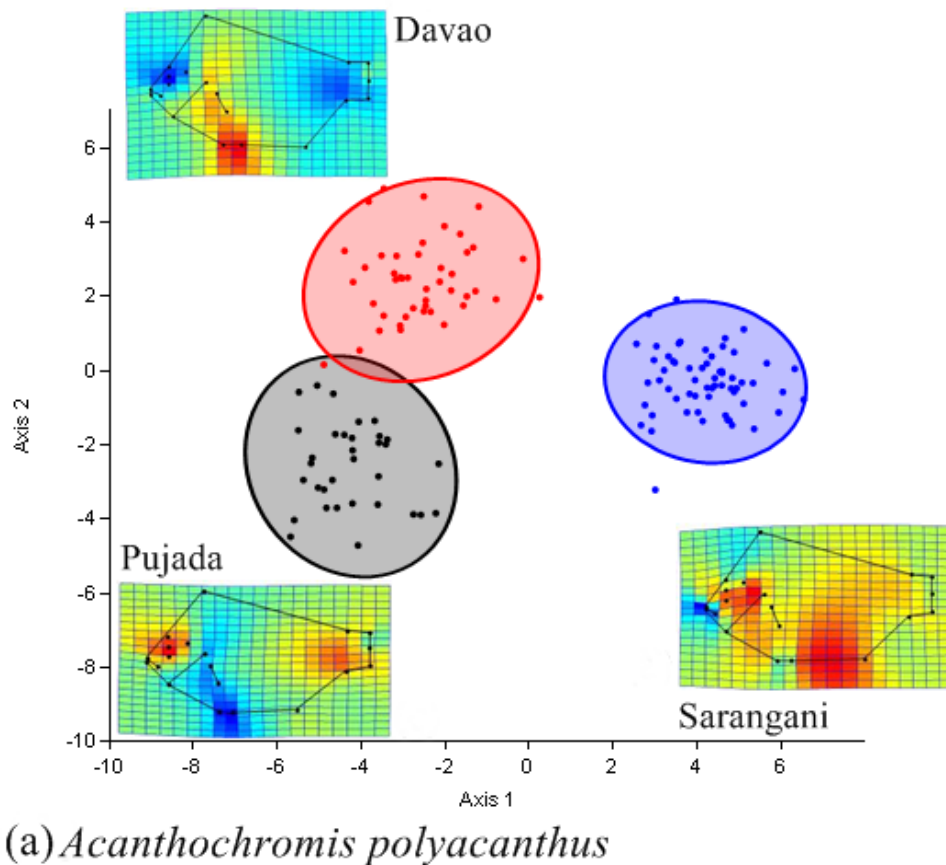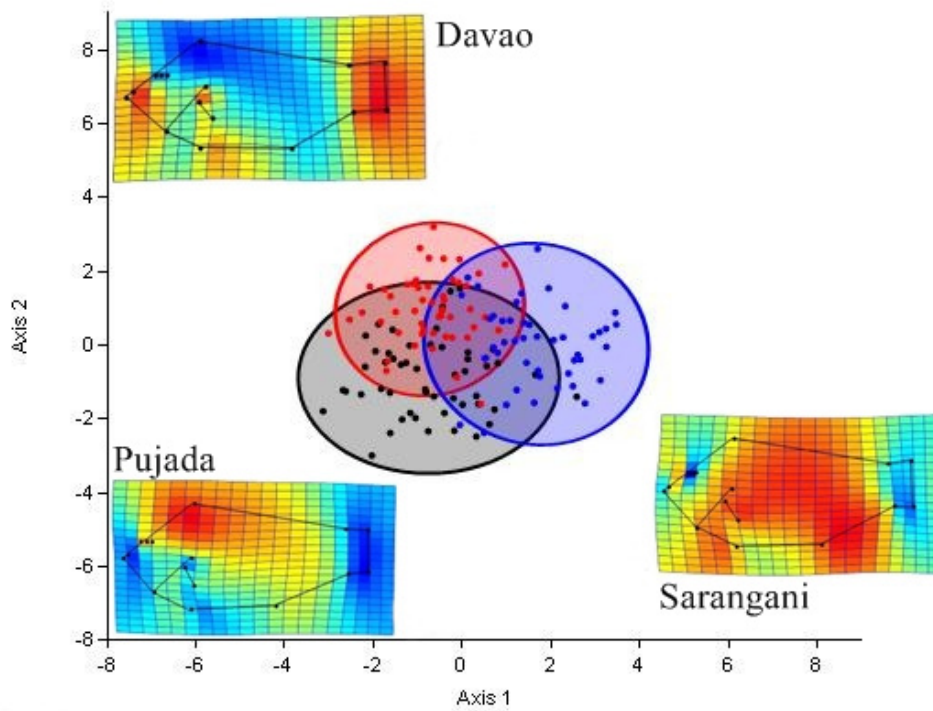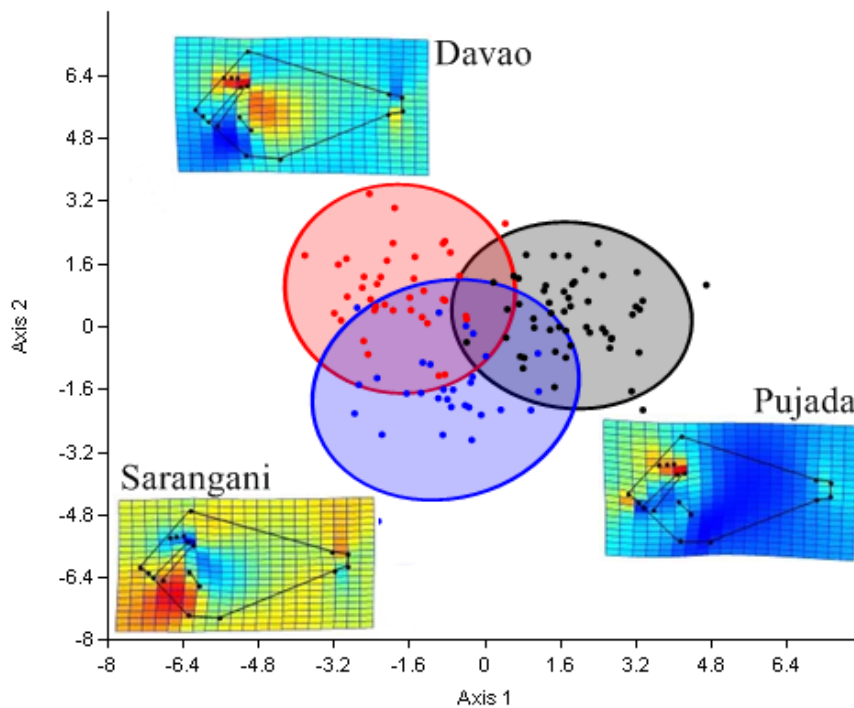

Fig. 3 Clustering of individuals into groups using 95% ellipses of canonical variates analysis indicating relationships among populations of (a) *Acanthochromis polyacanthus*. Blue (Sarangani), Red (Davao) and Black (Pujada) with relative warps showing expansion (red shade) and contraction (blue shade).   [continued to next page]

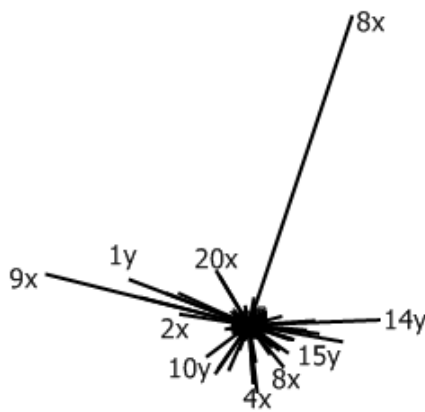(b) *Scarus quoyi*

(c) *Naso lituratus*

Fig. 3 continued. Clustering of individuals into groups using 95% ellipses of canonical variates analysis indicating relationships among populations of (b) *Scarus quoyi* (c) *Naso lituratus*. Blue (Sarangani), Red (Davao) and Black (Pujada) with relative warps showing expansion (red shade) and contraction (blue shade).

Naso lituratus

Overlapping of clusters was observed in the populations of *N. lituratus* indicating shared morphological features among the sampled specimens (Fig. 3c). Separation in axis 1 was observed as shape modifications in the body, putting an emphasis on the consistent expansion of most body parts in Sarangani Bay samples. In axis 2, variation was evident in the mouth, and similar to the findings in *S. quoyi*, *N. lituratus* samples from Pujada Bay also displayed contracted pectoral and caudal fins but elongated or tapered in Davao Gulf.

Statistical analyses

Despite overlapping in the CVA plots of *S. quoyi* and *N. lituratus*, MANOVA (Wilks' lambda and Rao's F) with all three populations of each species showed significant differences: *A. polyacanthus* (Λ=0.0132, $F_{72,202}$ = 21.64, p<0.01), *S. quoyi* (Λ=0.263, $F_{56,236}$ = 4.004, p<0.01), and *N. lituratus* (Λ=0.121, $F_{64,174}$ = 5.103, p<0.01). Post hoc test using Bonferroni further displayed significant differences between and among sites (Table 1). Biplot analysis revealed concordant results with the relative warps as indicated by the lengths of the vector: *A. polyacanthus* (1-mouth, 9-pelvic fin) (Fig. 4a), *S. quoyi* and *N. lituratus* (1-mouth, 9-pectoral fin) (Fig. 4b-c). Other major shape changes were observed in the biplot vectors of the following landmarks: A. *polyacanthus* for landmarks 8 (anal fin) and 14 (operculum), *S.quoyi* for landmarks 3 (dorsal fin), 7 (anal fin), and 12 (operculum), and *N. lituratus* for landmarks 2 (dorsal fin), 12(operculum) and 14 (pre-opercular opening) (Fig. 4, Table 2).
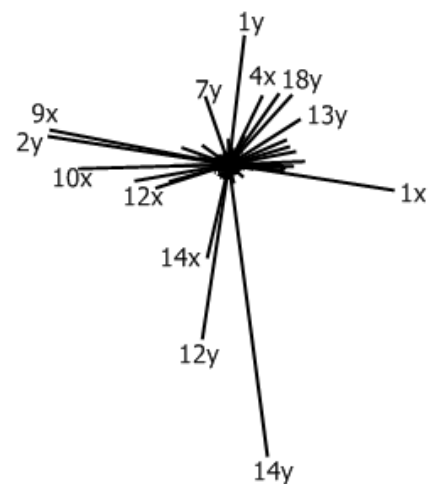

(a) *Acanthochromis polyacanthus*

Fig. 4 Biplot of principal component analysis showing the deviation of morphological landmarks from a common central axis (a) *Acanthochromis polyacanthus* (b) *Scarus quoyi* (c) *Naso lituratus.*
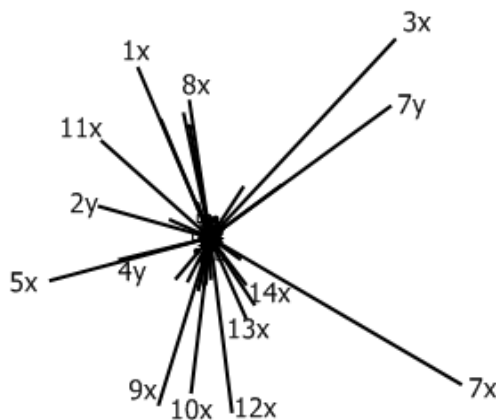
(b) *Scarus quoyi*

(c) *Naso lituratus*

Table 1 Comparisons of populations of three reef fish species (Results of Hotelling's pairwise comparison tests with Bonferroni corrections). *$P<0.05$

Species	Population 1	Population 2	
Acanthochromis polyacanthus			
	Davao	Pujada	*
	Davao	Sarangani	*
	Pujada	Sarangani	*
Scarus quoyi			
	Davao	Pujada	$P=0.003$
	Davao	Sarangani	*
	Pujada	Sarangani	*
Naso lituratus			
	Davao	Pujada	*
	Davao	Sarangani	$P=0.01$
	Pujada	Sarangani	*

Table 2 Sequence and corresponding landmarks of the digitized morphological characters

landmark number	*Acanthochromis polyacanthus*	*Scarus quoyi*	*Naso lituratus*
1	mouth (upper lip)	mouth (end)	mouth (end)
2	base of dorsal fin	base of dorsal fin	base of dorsal fin
3	end of dorsal fin	end of dorsal fin	end of dorsal fin
4	tail fin (upper)	tail fin (upper)	tail fin (upper)
5	tail fin (lower)	tail fin (lower)	tail fin (lower)
6	middle of 4 & 5	anal fin (end)	anal fin (end)
7	anal fin (end)	anal fin (base)	anal fin (base)
8	anal fin (base)	pelvic fin (base)	pelvic fin (base)
9	pelvic fin (end)	pectoral fin (end)	pectoral fin (end)
10	pelvic fin (base)	pectoral fin (base)	pectoral fin (base)
11	pectoral fin (end)	opercular opening	opercular opening
12	pectoral fin (base)	end of operculum	end of operculum
13	opercular opening	eye diameter	preopercular opening base
14	end of operculum	eye center	preopercular opening end
15	preopercular opening	eye diameter	eye diameter
16	mouth (lower lip)	mouth opening	eye center
17	mouth opening	n/a	eye diameter
18	eye center	n/a	mouth opening
19	eye diameter	n/a	n/a
20	eye diameter	n/a	n/a

Discussion

Significant differences among populations of the three reef fishes in this study add to the many list of studies involving intraspecific polymorphism at small spatial scales (Bagherian & Rahmani 2009, Omonoyi & Agbon 2008), with most differentiations attributed to shape modification. This is concordant with recent findings that diversification in reef fishes has been preceded by evolutionary changes in body shape (Claverie & Wainwright 2014).

According to Cavalcanti, Monteiro & Lopes (1999), the primary component of shape change concerned the arching of specimen's body, which was attributed by Carpenter (1996) to either measurement artifact as a result of sample

preservation or a functional interpretation. Considering that this study has not used any preservation technique and conducted all morphometric analysis on fresh samples, the observed shape modification among individuals is likely to have functional explanations.

Morphological differences associated with changes in body shape may be related to nutrition and fitness. In reef systems, more food resources favor positive growth (Jones 1986); hence broader body shapes were consistently observed in all Sarangani Bay samples in contrast to more slender shapes in Davao Gulf and Pujada Bay.

Sarangani Bay has major rivers with a large input of nutrients and sediments, especially to the north of the bay (de Jesus *et al.* 2001). In general, the area lacks typhoon but strong winds that allow vertical mixing and dilution (Peñaflor *et al.* 2007, Villanoy *et al.* 2011) prevail during the southwest monsoons, enhancing phytoplankton growth and the dominance of planktivores such as *A. polyacanthus*. Faster growth and development in *A. polyacanthus* could also be due to transfer of vital hormones during "glancing" (Kavanagh 1998), which may have been enhanced by environmental conditions currently present in the area. Also, the bay generally has higher algal cover reaching up to 25%

(Aliño *et al.* 2002), indicating a greater amount of food for herbivores like *S. quoyi* and *N. lituratus* in Sarangani.

In terms of fitness, individuals that developed larger features as in Sarangani, would likely have competitive advantages to escape its predators (Arreglado *et al.* 2013) as well as to allow capture of larger prey items (Doherty & Mccarthy 2004). In comparison, slender bodies of fishes in Davao Gulf and Pujada Bay may have developed as an efficient strategy for searching prey as in Arctic chars (Doherty & Mccarthy 2004), or as an increase in steady swimming performance as in Shemaya fishes (Bagherian & Rahmani 2009).

Aside from intraspecific variations in body shape, divergent forms were also observed in the buccal region of all three species, which could be due to differences in feeding habit and prey capture modes. Disparities in the structure of jaws in *Xanthicthys ringens* was a result of feeding predominantly on plankton at La Parguera in Puerto Rico, while grazing on benthic organisms in another site close by, Mona; a strategy believed to help reef fishes thrive in a wide array of habitat types (Turingan, Wainwright & Hensley 1995). Likewise, in Sarangani Bay, development of a relatively shorter snout by *A. polyacanthus* (Fig. 3a) might be an adaptation due to resource availability in the area.

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Scarid and acanthurid species like *S. quoyi* and *N. lituratus*, respectively, mainly feed on firmly attached prey (e.g epilithic algae, sponges, and sclerectinian coral polyps) by scraping the substrates (Wainwright & Bellwood 2002). With this behavior, differences in the mouth of both species between Davao Gulf and Pujada Bay populations (Fig. 3b-c) may be considered as resulting from contrasting substrate types in the two areas. *Porites* and *Millepora* were dominant corals in Davao Gulf, while *Montipora* and *Acropora* were dominant in Pujada Bay's coralline tidal flats. Differences in mouth morphology due to feeding habits had also been previously described by Marcus (1986) in Nigerian herring, *Ilisha africana* and more recently in an endemic African cichlid, *Sarotherodon melanotheron* (Omonoyi & Agbon 2008).

The variations in fin morphology can be linked to movement and swimming behavior of fish species. In reef fish evolution, high power caudal propulsion (i.e. Actinopterygii) is a more ancient evolutionary character than non-caudal slow swimming features (Acanthopterygii) (Webb 1982). As observed in this study, specific swimming behaviour in the three species may be associated with modifications in their caudal fins.

Additionally, the results of shape deformations (Fig. 3) further suggest that fins may have been modified for specialized function. For instance, the pelvic fins, which are

used for strong attachment, were only observed to differ in *A. polyacanthus*. *A. polyacanthus* is territorial and often stay close to the corals and other substrates, thus, a suitable design of pelvic fin indicates a favorable adaptation when sudden changes in current occurs. But for highly mobile reef fishes, where swimming behavior is highly dictated by ambient water velocity (Binning, Roche & Fulton 2014), differences would be more expected in the pectoral fin as it helps the fish create dynamic forces to maintain depth and enhance locomotor performance (Gerstner 1999). Pectoral fin shape affects swimming performance due to biomechanical constraints (Binning, Roche & Fulton 2014): species with tapered fins are faster steady swimmers that often dominate high-flow wave swept habitats, whereas those with rounded fins are better at maneuvering in low-flow sheltered reefs (Webb 1994, Fulton & Bellwood 2004, Binning, Roche & Fulton 2014). This study has shown similar findings for both *S. quoyi* and *N. lituratus*: tapered or elongated pectoral fins were more prominent in a site exposed to strong current and wave action, Davao Gulf, in comparison to Pujada Bay where currents are weaker.

Other polymorphic traits have been noted in the biplot vectors which include the dorsal and anal fins, and the operculum. Contrasting features of the dorsal fins may relate to varying protection against turning and rolling, while the differences in anal fins may be due to stabilization

techniques during swimming. The operculum and preopercular openings of reef fishes function as a seal to prevent reverse water flow from occurring during respiration and, thus, are vital in obtaining oxygen. This essential function suggests that the divergence of the form could be a response to different levels of siltation or of dissolved oxygen in the areas.

Although reef fish populations in Pujada, Davao and Sarangani may implicitly be connected due to the strong influence of the Mindanao current, the exposure to varying environmental conditions may have induced morphological differentiations observed in this study. The disparities in shape and length of morphological landmarks suggest adaptive responses of organisms to their natural habitats. It is not clear however, whether genetic mutation also plays a role in this differentiation, thus, investigations involving genetic tools may also be done to elucidate these relationships.

Acknowledgments

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