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FEATURE ARTICLE

Morphologically plastic responses to shading in the zoanthids *Zoanthus sansibaricus* and *Palythoa tuberculosa*

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Abstract Zoanthids of the order Zoantharia (Anthozoa: Hexacorallia) exhibit high intraspecific morphological variability, but whether this is due to polymorphism, phenotypic plasticity or a combination of both remains unknown. To address this knowledge gap, in November 2010, eight colonies each of *Zoanthus sansibaricus* and *Palythoa tuberculosa* were sampled from three reefs off the south of mainland Singapore and transplanted to a shallow experimental site. The colonies were then distributed under two types of treatment frames: control and shaded. After 87 days, morphometric characters were extracted from macro-images. Reaction norms, principal components analysis, analysis of variance and canonical discriminant analysis all demonstrated light-induced changes in morphology. Patterns of plastic changes were similar for both species: shaded colonies had larger polyps as compared to control colonies. The presence of plastic responses in zoanthids may facilitate their colonization of a broad range of habitats as well as help them to withstand temporal changes in their environment.

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Introduction

Zoanthids of the order Zoantharia are colonial cnidarians in the class Anthozoa, subclass Hexacorallia (Ruppert et al. 2003). The order contains at least 17 genera, six of which contain zooxanthellae of the genus *Symbiodinium* in their polyps. The two most common zoanthid zooxanthellate families are the Sphenopidae, which incorporate sand and other tiny debris in their coenenchyme (Haywick and Mueller 1997), and the Zoanthidae, which are non-encrusting. The genera *Palythoa* (Sphenopidae) and *Zoanthus* (Zoanthidae), studied here, are widely distributed in tropical and subtropical coral reef environments throughout the world. Despite their abundance, the ecology of zoanthids remains little known, being one of the least examined groups within the phylum Cnidaria (Sinniger et al. 2008; Reimer and Todd 2009; Reimer et al. 2012). Past methods of zoanthid classification involved the comparison of different characters such as internal mesenteries and septa (Herberts 1987); tentacle counts (Herberts 1972); nematocyst type and distribution (Ryland and Lancaster 2003, 2004); polyp morphologies, and coenenchyme characteristics (Pax 1910). Reimer et al. (2004) highlighted the difficulty in identifying *Zoanthus* species based on morphology alone as zoanthids exhibit high morphological variability. The taxonomy of both *Zoanthus* and *Palythoa* has been re-examined recently by using molecular techniques and morphological data to better discern the phylogenetic and evolutionary relationships of their species (Burnett et al. 1995, 1997; Reimer et al. 2006b, c, d, 2007). However, whether the intraspecific variation displayed by many species is due to genetic differences phenotypic plasticity or a combination of both remains unknown.

Phenotypic plasticity refers to when a genotype is able to produce different phenotypes (e.g. morphology, physiology, life history and/or behaviour) in different environments (Bradshaw 1965; Scheiner 1993; Garland and Kelly 2006). Plastic responses by a sessile marine organism can help it to adjust to spatially heterogeneous and/or temporally unpredictable conditions (Todd 2008). Responses may include reversible and irreversible changes in the organism's development (Hoffmann and Parsons 1991) and can be active (the change in phenotype mitigates the effect of a sub-optimal environment) or passive (change is simply a function of shifts in resource availability) (Schlichting 1989). Reaction norms are graphical representations of genotypic responses to new environments and are a common way of visualizing plasticity (Stearns 1989; Bruno and Edmunds 1997; Schlichting and Pigliucci 1998). At the population level, the phenotypic plasticity of a species tested in two environments is measured as the difference between the population mean in each (Via 1993) to produce 'mean norms of reaction'. The rate and direction of the evolution of a mean norm of reaction is determined by the additive genetic variation for plasticity within a population (Via and Lande 1985; DeJong 1990; Scheiner 1993). Even though phenotypic plasticity has been documented in molluscs (Trussell 2000), echinoderms (Ebert 1996), crustaceans (Mokady et al. 1999), bryozoans (Okamura 1992) and corals (Foster 1979; Bruno and Edmunds 1997; Muko et al. 2000; Todd et al. 2002a, b, 2004a; Hoeksema 2012), no published papers have specifically examined the phenotypic plasticity in zoanthids.

Similar to corals, reef zoanthids are mostly broadcast spawners, periodically releasing gametes into the water (Hirose et al. 2011). Once larvae settle and metamorphose, they cannot escape their immediate surroundings and are therefore committed to that particular microhabitat (Todd 2008). Adaptation through genetic change can be of limited benefit to a young colony experiencing a novel and dynamic coral reef environment; but, in a species frequently experiencing such (disruptive) conditions, phenotypic plasticity may evolve (Bradshaw 1965). Light availability in particular can greatly affect photosynthetic organisms such as corals and zoanthids as it is directly related to the primary production of endosymbiotic zooxanthellae (Davy et al. 1996). Consequently, the daily carbon acquisition of the host is light-dependent and a reduction in irradiance may cause detrimental effects to its growth and survival. In conditions of low light intensity, coral colonies sometimes become explanate in order to capture light more efficiently (Dustan 1975; Graus and Macintyre 1982). Correspondingly, convoluted forms which have larger surface areas can develop in conditions of high light intensity (Willis 1985; Muko et al. 2000). Reduction in light has also been shown to cause small-scale morphological plasticity in coral corallite and polyp structure (Bruno and Edmunds 1997; Muko et al. 2000; Todd et al. 2004b). Todd et al. (2004a) demonstrated that corallites in the massive coral *Favia speciosa* had a greater 'depth' when transplanted to shallow water compared with those transplanted to deeper water. The function of such morphological changes in relation to light was tested in a study by Ow and Todd (2010). Corallites of *Goniastrea pectinata* with deeper calices were more efficient at shading, thus protecting the underlying tissue from high irradiance (and possibly associated ultraviolet radiation), whereas corallites with shallower calices were more efficient in light capture for photosynthesis (Ow and Todd 2010). As reef zoanthids are also light-dependent cnidarians, it is possible different light regimes can similarly induce morphological changes in this group.

Transplant experiments, in which organisms are introduced into new habitats and their responses measured after a period of time, are an effective way of testing for environmental influences on morphology (Schmid 1985; Todd 2008; Otaki et al. 2012). A number of studies have examined population plasticity in corals by removing whole coral colonies from their natal environment and transplanting them to new habitats (e.g. Foster 1979; Graus and Macintyre 1982; Willis 1985; Gleason 1992). These experiments can identify population × environment interactions, that is, they determine whether populations respond differently to the same environmental conditions. In the present study, colonies of two zoanthid species, *Zoanthus sansibaricus* and *Palythoa tuberculosa*, from three reefs within Singapore's Southern Islands were transplanted to a shallow experimental site at Pulau Hantu and placed under two types of shading frames: control and shaded. After 87 days, morphological data were extracted from multiple macro-images taken of the colonies. Multivariate analyses were conducted to determine differences between treatments, among populations, and possible population × treatment interactions. The two hypotheses tested were as follows: (1) small-scale changes in morphology can be environmentally induced in zoanthids; and (2) there exists among-population variation for the levels of plasticity expressed.

Materials and methods

To test the effect of reduced light on *Z. sansibaricus* and *P. tuberculosa*, colonies were collected from three reefs among Singapore's Southern Islands (Fig. 1). All colonies were transplanted to an experimental site at Pulau Hantu where they were positioned under open (control) and shaded (treatment) frames and left for approximately 3 months. The methodology is described in detail below.

Singapore and its marine environment

Singapore is located approximately 1° north of the equator, at the southern tip of peninsular Malaysia. It has a hot and humid tropical climate all year round with two monsoon periods from June to August (mild south-west monsoon) and from November to February (wetter north-east monsoon). Due to the protection provided by surrounding land masses (Peninsula Malaysia and Sumatra, Indonesia), Singapore's coastal environment is of a low energy type characterized by accumulation rather than erosion (Swan 1971). Numerous patch reefs can be found in the waters south of the mainland, and many of the small islands have fringing reefs (Hilton and Chou 1999). However, construction, dredging and land reclamation activities have led to chronic levels of sedimentation over the last few decades which have resulted in a dramatic reduction in underwater visibility (Chou 1996; Todd et al. 2010). The increase in sediments and decrease in light levels have resulted in very little zooxanthellate coral cover below 8 m depth.

Sampling and study sites

Pulau Tekukor (01°13′59.39″N, 103°50′12.92″E) is situated 4 km from mainland Singapore (Fig. 1). The island is subjected to the effects of nearby construction and reclamation activities. Currents flowing away from shore, however, remove sediments from the reef flat (Low and Chou 1994).

Pulau Tembakul (Kusu Island) (01°13′31.78″N, 103°51′31.56″E) is situated 5 km from mainland Singapore and is the eastern-most island along the Singapore Strait (Fig. 1). With open sea and a major shipping fairway to the east, the site periodically experiences both bottom sediment disturbance caused by ship wakes and strong tidal currents flowing in an east–west direction. There are higher sedimentation rates here compared to the other two study sites (Low and Chou 1994).

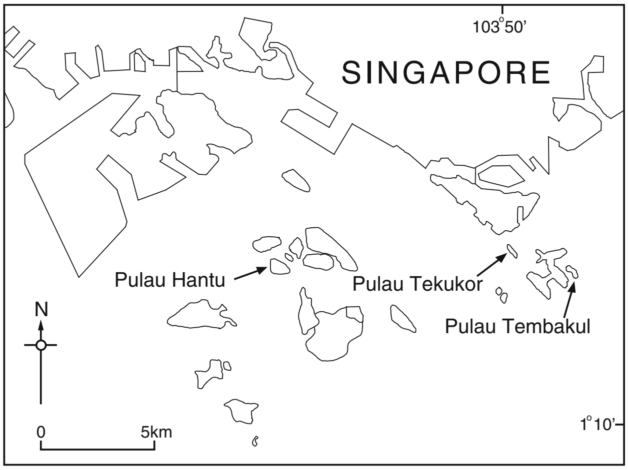

Fig. 1 Zoanthids were collected from fringing reefs at Pulau Hantu, P. Tembakul and P. Tekukor. The experiment was conducted at P. Hantu

Pulau Hantu (01°13′36.87″N, 103°44′48.74″E) is situated 6 km from mainland Singapore and is surrounded by other offshore islands and patch reefs that reduce the power of incoming waves. Pulau Hantu was used as the experimental site where all sampled colonies were transplanted to (Fig. 1). To minimize the effects of water movement, we chose the reef flat at the north-west of the island as it is sheltered by a nearby patch reef—creating a very low-energy environment (Todd et al. 2004a).

Study species

Zoanthus sansibaricus Carlgren 1900, is usually associated with coral reef substrates in shallow tropical and subtropical waters exposed to strong water currents and/or wave action (Reimer et al. 2006b), but it is often found in Singapore in calmer habitats (Reimer and Todd 2009). Colonies have a dark purple outer surface with liberae polyps (Pax 1910) that are free of the coenenchyme (Fig. 2a). Each polyp is slightly wider in diameter towards the oral opening than at the base and possesses 48–60 brown or dark green tentacles (Reimer and Todd 2009). The oral disc is 2–8 mm in diameter and varies widely in colour (e.g. red, blue, white, light to dark green, orange, brown, grey) and fluorescent patterning. This species does not incorporate sand into its coenenchyme.

Palythoa tuberculosa Esper 1805, thrives in tropical and subtropical areas (Reimer et al. 2006a) and can be commonly found growing on rocks or coral rubble in shallow waters around Singapore (Reimer and Todd 2009). Colonies resemble a light to dark brown rubber mat with polyps generally embedded in the coenenchyme (Fig. 2b). Each polyp has a thick and short body column with a brown, tan or cream oral disc edged with 38–52 brown tentacles in two rows; the oral disc is 6–16 mm in diameter (Reimer and Todd 2009). *Palythoa* spp. are known to incorporate fine sand and other tiny debris into their well-developed coenenchyme to provide structural support for the colony (Haywick and Mueller 1997).

Experimental design

Square frames measuring 1.0 m (length) × 1.0 m (width) × 0.6 m (height) were constructed using plumbing-type PVC pipes. In order to create shade, three layers of 17-mm plastic mesh were cable-tied to the frames to create light levels of ∼43 % surface irradiance (Chen 2010). This approach of using multiple layers of open mesh is more effective than using the traditional (garden) shade

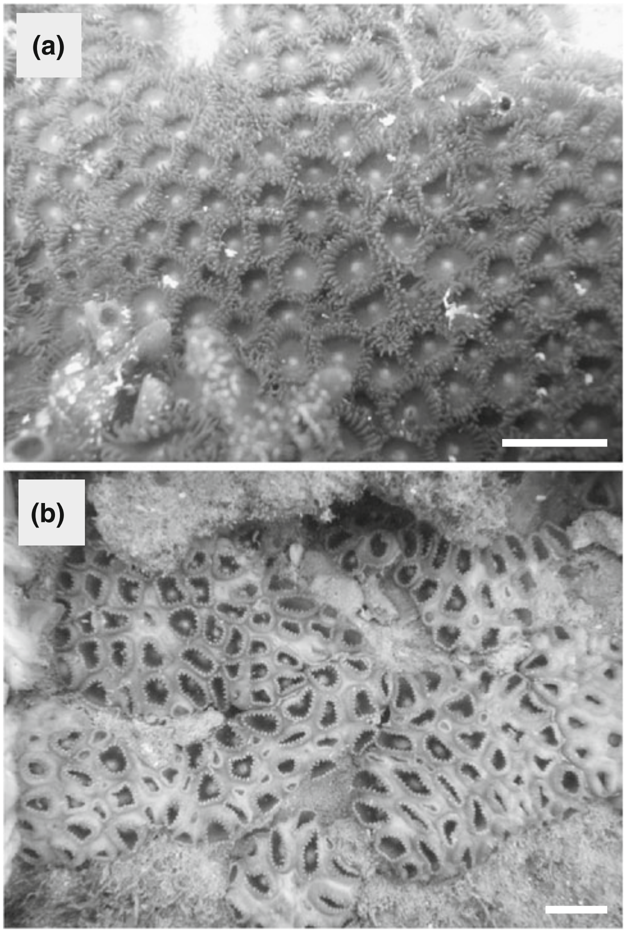

Fig. 2 The two study species: **a** *Zoanthus sansibaricus* and **b** *Palythoa tuberculosa*. *Scale bars* 1 cm

netting that rapidly fouls in Singapore's turbid marine environment. Four replicate frames of the control and shaded treatment were deployed alternately along the reef flat at Pulau Hantu ~2 m below mean sea level. No plastic mesh was attached to the control frames. All frames were secured to angle irons that had been hammered into the substrate.

Eight colonies (size 40–50 cm^2) of *Z. sansibaricus* and eight colonies (size 80–100 cm^2) of *P. tuberculosa* were haphazardly sampled from 1 to 3 m depth from each of the three reefs described above: Pulau Tekukor, P. Tembakul and P. Hantu, and transplanted to the experimental site at P. Hantu (Fig. 2). Each colony was attached to a 10 cm × 10 cm acrylic tile with underwater epoxy. Sets of six colonies (three reefs × two species) were then cable-tied randomly (using random number tables and a grid formation) to a perforated but rigid plastic platform. All colonies-on-platforms were left on the reef at P. Hantu for a week of acclimation before they were finally secured under the frames. Thus, each of the eight frames was positioned over a cluster of six colonies, that is, 48 colonies in total (24 under shade and 24 open control).

The experiment commenced on 19 November 2010. The colonies and frames were checked and maintained every 2 weeks. Sediment and algae from surrounding surfaces were removed using nylon brushes. On 14 February 2011 (after 87 days), multiple in situ macro-images were taken of the colonies (first with open polyps and then with closed polyps) using a digital camera (Canon PowerShot S90) in an underwater housing. This represented the termination of the field experiment. Following Todd et al. (2001, 2004c), all suitable polyps (i.e. those which were perpendicular to the camera and in sharp focus) were identified from the images and individually numbered. Using random number tables, five polyps were selected for morphological measurement and the mean of the five values used as the replicate in subsequent analyses. A total of nine polyp characters were obtained (Table 1) and analysed using Coral Point Count V4.0 with Excel extensions image-analysis software (National Coral Reefs Institute) (Kohler and Gill 2006).

Statistical analyses

Reaction norms were used to visualize the responses of colonies to shade as well as help identify population × environment interactions (Stearns 1989). Mean character trait values for each population were plotted against the environmental signal, i.e. shade and control (Schlichting and Pigliucci 1998). Different populations were hypothesized to have different reaction norms. Parallel reaction norms indicate population + environment, whereas crossing reaction norms have different gradients and indicate population × environment interactions (Stearns 1989; Schlichting and Pigliucci 1998).

For all polyp characters, normality and homogeneity of variance were tested using, respectively, Kolmogorov–Smirnov and Levene's tests. Data that did not meet these assumptions were $\log^{10}$-transformed. Principal component analysis (PCA) (Hotelling 1933) was conducted on the nine characters in order to reduce the dimensionality of the data and provide compound variables for further analysis. After again testing for normality and homogeneity of variance, scores on the first three PCs for each colony were used as response variables in a two-way analysis of variance (ANOVA) to determine any morphometric differences between treatments, among populations, and treatment × population interactions. Treatments were considered as fixed factors, whereas population was treated as a random factor. As PC 1, 2 and 3 were independent, Bonferroni corrections were not used to correct the nominal alpha.

Standard stepwise canonical discriminant analysis (CDA) was performed on polyp character means to

Table 1 Morphological characters, units and means (±SE) for each treatment and population of *Zoanthus sansibaricus* and *Palythoa tuberculosa*

Character	Unit	Colonies from Pulau Hantu		Colonies from Pulau Tembakul		Colonies from Pulau Tekukor	
		Unshaded	Shaded	Unshaded	Shaded	Unshaded	Shaded
Zoanthus sansibaricus							
Oral disc area (ODA)	cm^2	0.11 ± 0.02	0.25 ± 0.06	0.10 ± 0.06	0.14 ± 0.02	0.16 ± 0.04	0.19 ± 0.04
Mean tentacle length (MTL)	cm	0.15 ± 0.03	0.15 ± 0.02	0.09 ± 0.03	0.10 ± 0.02	0.16 ± 0.04	0.12 ± 0.02
Maximum oral disc length (ODMAX)	cm	0.41 ± 0.03	0.56 ± 0.08	0.40 ± 0.10	0.43 ± 0.03	0.48 ± 0.06	0.51 ± 0.07
Minimum oral disc length (ODMIN)	cm	0.35 ± 0.03	0.51 ± 0.08	0.33 ± 0.10	0.37 ± 0.03	0.41 ± 0.05	0.43 ± 0.06
Area of closed polyp (CPA)	cm^2	0.07 ± 0.01	0.09 ± 0.02	0.08 ± 0.03	0.08 ± 0.01	0.12 ± 0.03	0.14 ± 0.03
Maximum closed polyp length (CPMAX)	cm	0.30 ± 0.02	0.35 ± 0.03	0.31 ± 0.06	0.33 ± 0.02	0.41 ± 0.06	0.43 ± 0.05
Minimum closed polyp length (CPMIN)	cm	0.27 ± 0.02	0.32 ± 0.03	0.29 ± 0.07	0.29 ± 0.02	0.35 ± 0.05	0.38 ± 0.05
Inter-polyp distance (IPD)	cm	0.10 ± 0.02	0.14 ± 0.02	0.15 ± 0.02	0.14 ± 0.03	0.11 ± 0.02	0.15 ± 0.03
Tentacle count (TC)	count	48.10 ± 1.71	48.30 ± 1.40	45.87 ± 0.35	49.90 ± 2.81	45.73 ± 1.04	46.50 ± 1.18
Palythoa tuberculosa							
Oral disc area (ODA)	cm^2	0.39 ± 0.02	0.42 ± 0.07	0.27 ± 0.09	0.44 ± 0.15	0.53 ± 0.02	0.55 ± 0.09
Mean tentacle length (MTL)	cm	0.10 ± 0.00	0.10 ± 0.01	0.08 ± 0.01	0.11 ± 0.01	0.11 ± 0.01	0.10 ± 0.01
Maximum oral disc length (ODMAX)	cm	0.79 ± 0.02	0.76 ± 0.08	0.61 ± 0.09	0.76 ± 0.15	0.90 ± 0.03	0.88 ± 0.08
Minimum oral disc length (ODMIN)	cm	0.61 ± 0.02	0.66 ± 0.06	0.53 ± 0.08	0.65 ± 0.13	0.72 ± 0.01	0.75 ± 0.06
Area of closed polyp (CPA)	cm^2	0.27 ± 0.03	0.23 ± 0.03	0.20 ± 0.07	0.34 ± 0.08	0.28 ± 0.03	0.40 ± 0.03
Maximum closed polyp length (CPMAX)	cm	0.64 ± 0.04	0.56 ± 0.04	0.52 ± 0.10	0.71 ± 0.10	0.66 ± 0.04	0.76 ± 0.04
Minimum closed polyp length (CPMIN)	cm	0.51 ± 0.03	0.50 ± 0.03	0.44 ± 0.07	0.59 ± 0.07	0.52 ± 0.02	0.64 ± 0.03
Inter-polyp distance (IPD)	cm	0.11 ± 0.01	0.19 ± 0.03	0.13 ± 0.02	0.21 ± 0.04	0.12 ± 0.01	0.20 ± 0.02
Tentacle count (TC)	count	44.30 ± 1.15	41.10 ± 0.99	36.30 ± 3.90	39.73 ± 3.10	48.00 ± 1.26	48.40 ± 1.21

illustrate the overall morphological differences between shaded and control colonies (Sokal and Rohlf 1995). CDA also reduces the data dimensionality and provides canonical variables (linear combinations of polyp characters) that summarize variation between groups. Wilks's lambda test (a multivariate test which has a similar role to *F* test) was performed to assess the presence of differences between groups and the homogeneity within groups (Hair et al. 2006). Unlike forward and backward stepwise CDA, standard stepwise CDA does not remove characters which contribute least to group separation. For each species, six 'populations' (three natal reefs × two treatments) were entered into the analysis. All statistical analyses were conducted using STATISTICA V8 (Statsoft®).

Results

All colonies except two *Z. sansibaricus* and one *P. tuberculosa* survived the transplantation and shading experiment. Only the surviving colonies were used in the analyses. Qualitatively, shaded *P. tuberculosa* polyps were taller and extended beyond the coenenchyme more than unshaded polyps, which remained in their relatively 'embedded' (=immersae) form. The polyps from shaded colonies of *Z. sansibaricus* were spaced further apart compared to those of the unshaded colonies. Quantitative character means and standard errors for the different populations and treatments are summarized in Table 1. There were changes in various specific characters between treatments. Shaded colonies generally had larger polyp sizes (ODA, ODMAX, ODMIN, CPA, CPAMAX, CPMIN) in both species (Table 1) as reflected in the reaction norms (Figs. 3 and 4). The populations generally responded similarly to the difference in light conditions. However, some population × environment interactions can be seen for certain character traits. In *Z. sansibaricus* (Fig. 3), the specimens from Pulau Tekukor and P. Tembakul responded in the opposite direction for MTL and IPD, respectively. PC 2 character means increased for populations from P. Tekukor and P. Hantu, whereas the character mean decreased for the population from P. Tembakul. In *P. tuberculosa* (Fig. 4), the zoanthids from P. Tekukor and P. Tembakul responded differently for MTL and ODMAX, respectively. Also, shaded colonies from P. Hantu responded in the opposite direction for CPA, CPMAX, CPMIN and PC 3.

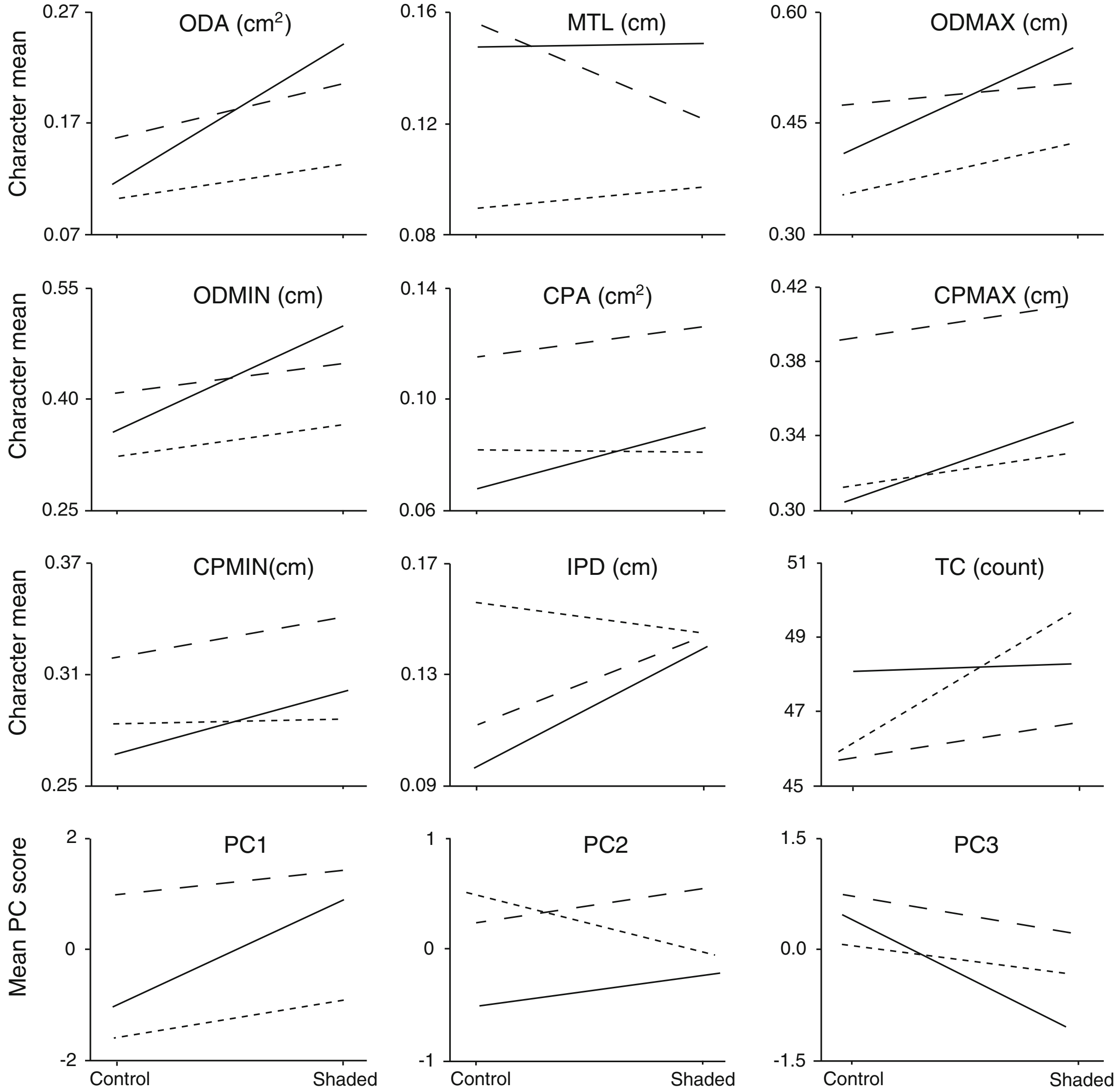

Fig. 3 Reaction norms for character means and PC scores for *Zoanthus sansibaricus*. Different lines show population origin: Pulau Hantu (*solid*), P. Tembakul (*dotted*), P. Tekukor (*dashed*). Character abbreviations are provided in Table 1

The principal component analysis (PCA) identified three factors which accounted for 89.4 % of the variance for *Z. sansibaricus* and 94.6 % of the variance for *P. tuberculosa*. There were significant differences in PC 3 scores between treatments for *Z. sansibaricus* whereas, for *P. tuberculosa*, there were significant differences between treatments and among populations for PC 2 scores and a significant treatment × population interaction for PC 3 (ANOVA results, Table 2).

For *P. tuberculosa*, canonical discriminant analysis (CDA) showed a strong separation (*P. tuberculosa* $\lambda = 0.00649$, $F = 2.0078$, $p < 0.0117$) between colonies maintained under the shaded and unshaded treatments, whereas there was more overlap for *Z. sansibaricus* ($\lambda = 0.00869$, $F = 1.6325$, $p < 0.0605$). Results for both species indicated the presence of multiple morphological differences between treatments (Fig. 5). The shaded populations for *P. tuberculosa* were grouped towards the negative region of the first canonical variable (CV 1), whereas the unshaded populations grouped towards the positive region of CV 1. However, for *Z. sansibaricus*, the split between the two treatments was more defined by the second canonical variable (CV 2). CPA and CPMAX had the greatest effect on group separation for *P. tuberculosa,* whereas CPA, CPMIN and ODMAX had the greatest effect on group separation for *Z. sansibaricus* (Tables 3 and 4).

Discussion

Population × environment interactions have been identified previously in plants (e.g. Schmid 1985; Schlichting

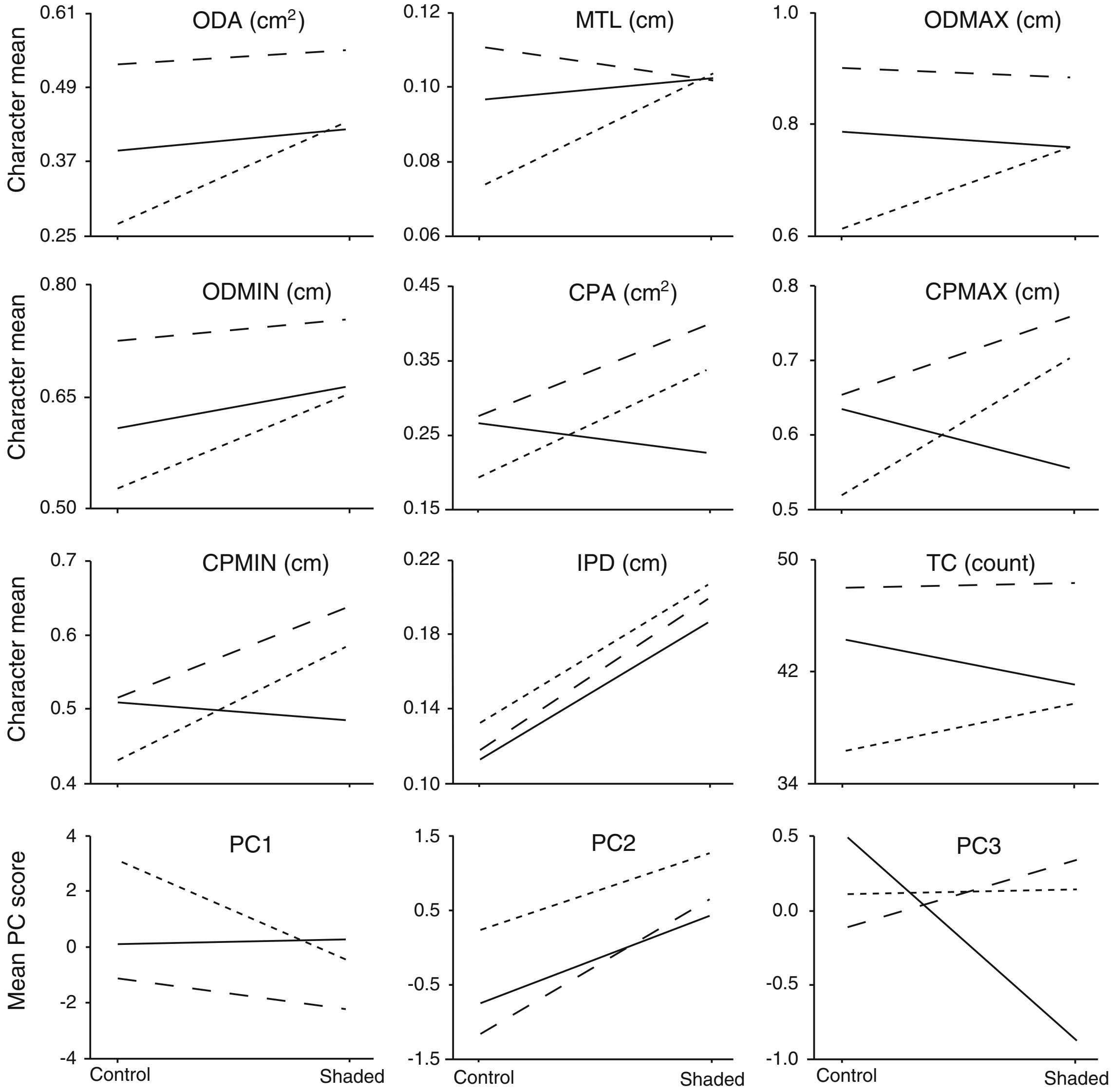

Fig. 4 Reaction norms for character means and PC scores for *Palythoa tuberculosa*. *Different lines* show population origin: Pulau Hantu (*solid*), P. Tembakul (*dotted*), P. Tekukor (*dashed*). Character abbreviations are provided in Table 1

1986), insects (e.g. Otaki et al. 2012), amphibians (Bernardo 1994; Relyea 2002), fish (Trexler et al. 1990; Trexler and Travis 1990) and corals (Foster 1979; Willis 1985). Here, for the first time, we demonstrate population × environment interactions in zoanthids. After 87 days of shading, the small-scale morphology of both *Z. sansibaricus* and *P. tuberculosa* changed. The reaction norms in Figs. 3 and 4 show that, in general, both species responded similarly with most characters under the shaded treatment increasing in size. ANOVAs based on PCA scores (PC 3 for *Z. sansibaricus*, and PC 2 for *P. tuberculosa*) showed significant differences between the (shaded) treatment and (unshaded) control. CDA results also indicated strong group separation between the shaded and unshaded colonies. Some reaction norms crossed, evincing the presence of among-population variation for the levels of plasticity expressed. The PC 3 score ANOVA results demonstrated a significant population × treatment interaction for *P. tuberculosa.*

Based on the significant differences identified by ANOVA (Table 2) and the stronger group separation illustrated by the CDA (Fig. 5), *P. tuberculosa* is more phenotypically plastic than *Z. sansibaricus*. Phenotypic plasticity is often associated with a generalist life strategy as it enables individuals to respond to, and survive in, more than one environment (van Tienderen 1991; Schlichting and Pigliucci 1998). It can also aid colonization, as shown for the annual plant *Xanthium strumarium* (Moran et al. 1981) and the ladybird beetle *Harmonia axyridis* (Grill et al. 1997). Both *P. tuberculosa* and *Z. sansibaricus* are

Table 2 ANOVA using scores from PC 1, 2 and 3 as traits

	df	PC 1			PC 2			PC 3		
		MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
Zoanthus sansibaricus										
Treatment (T)	1	6.451	1.201	0.289	0.056	0.034	0.856	3.592	6.859	0.019*
Population (P)	2	9.094	1.693	0.215	4.095	2.487	0.115	1.140	2.178	0.146
T × P	2	1.672	0.311	0.737	1.546	0.939	0.412	0.903	1.724	0.210
Residuals	16	5.372			1.647			0.524		
Palythoa tuberculosa										
Treatment (T)	1	12.688	2.412	0.139	10.182	24.948	0.000***	0.492	1.247	0.280
Population (P)	2	17.325	3.293	0.062	2.226	5.455	0.015*	0.255	0.648	0.536
T × P	2	6.545	1.244	0.313	0.331	0.810	0.461	1.803	4.571	0.026*
Residuals	17	5.261			0.408			0.394		

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

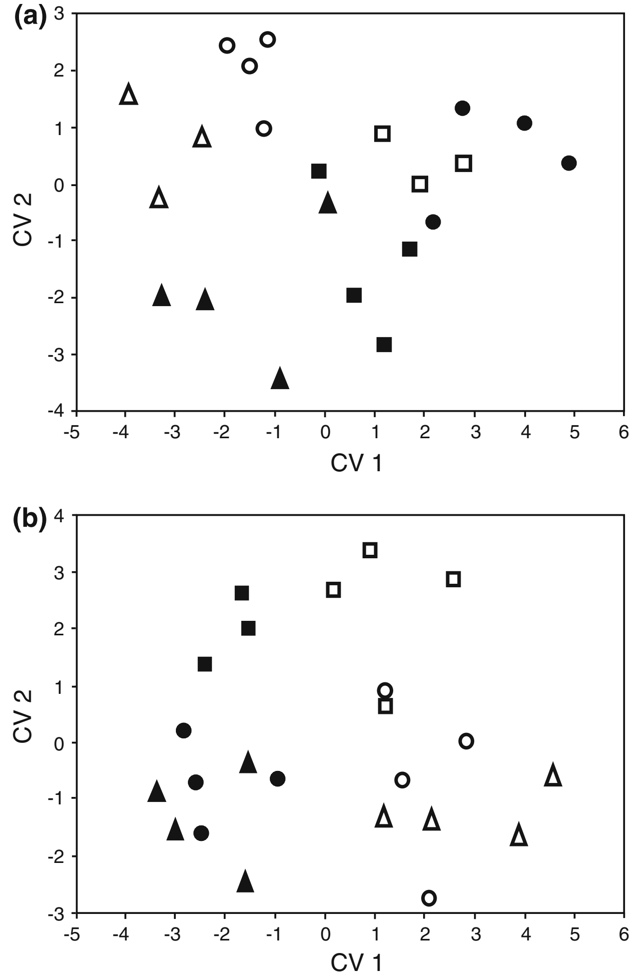

Fig. 5 CDA plots showing separation of treatments for: **a** *Zoanthus sansibaricus* and **b** *Palythoa tuberculosa. Solid points* shaded treatment; *open points* unshaded treatment. Colonies from the same natal site are represented by the *same shapes*: Pulau Hantu (*circles*), P. Tembakul (*squares*), P. Tekukor (*triangles*)

Table 3 Principal component (PC) scores for each character

Character	PC 1	PC 2	PC 3
Zoanthus sansibaricus			
ODA	0.902	−0.118	−0.377
MTL	0.720	−0.490	0.135
ODMAX	0.930	−0.156	−0.283
ODMIN	0.935	−0.165	−0.274
CPA	0.862	0.405	0.252
CPMAX	0.883	0.350	0.261
CPMIN	0.893	0.361	0.205
IPD	−0.252	0.685	−0.534
TC	0.064	−0.789	−0.039
Proportion of total	0.606	0.202	0.086
Palythoa tuberculosa			
ODA	−0.949	−0.201	−0.206
MTL	−0.852	−0.056	−0.257
ODMAX	−0.925	−0.305	−0.099
ODMIN	−0.931	−0.139	−0.273
CPA	−0.946	0.158	0.273
CPMAX	−0.935	0.120	0.317
CPMIN	−0.934	0.236	0.236
IPD	−0.470	0.827	−0.277
TC	−0.889	−0.247	0.130
Proportion of total	0.778	0.111	0.057

considered generalists, found as they are in a variety of depths and substrates, but *P. tuberculosa* is more common over a wider range of environments than *Z. sansibaricus* (Irei et al. 2011) and is potentially a good colonizer.

There are two, non-mutually exclusive, explanations for why the zoanthid populations from the three islands may respond differently to the same shading treatment (i.e. why

Table 4 Canonical variable (CV) scores for each character

Character	CV 1	CV 2	CV 3
Zoanthus sansibaricus			
ODA	4.355	1.511	2.793
MTL	−1.312	1.903	0.665
ODMAX	−11.225	−2.871	−0.714
ODMIN	8.503	0.286	−1.641
CPA	−3.371	−4.171	−3.434
CPMAX	0.065	−0.307	5.699
CPMIN	2.524	3.698	−2.577
IPD	0.491	−0.392	0.368
TC	0.786	−1.063	−0.211
Palythoa tuberculosa			
ODA	−3.143	−3.508	−8.943
MTL	0.501	0.097	−1.133
ODMAX	2.234	1.864	1.133
ODMIN	1.341	1.791	7.287
CPA	−17.605	−8.199	−3.754
CPMAX	11.850	7.104	1.257
CPMIN	5.105	2.036	2.785
IPD	−1.049	0.286	−0.181
TC	0.606	−1.650	1.674

there are population-specific norms of reaction). The first is simply that the populations had different genetic compositions leading to differential responses to treatments. Broadcast spawning by reef invertebrates generally leads to high dispersal and general mixing of genetic information (Veron 2000; Scheiner et al. 2012). In order for populations to have distinctive genotypes, it would require a lack of connectivity among reefs and the emergence of 'new' populations due to natural selection, genetic drift and/or mutation, founder effects, etc. Recent theoretical (Tay et al. 2012) and genetic (Neo and Todd 2012) work on the connectivity of Singapore's broadcast spawning marine invertebrates suggests that the flow of larvae and genes among local reefs may not be as high as expected for such a small area.

The second possible explanation is that differences in natal reef environments led to variation in how the zoanthid colonies responded to the two light treatments. For example, a colony from a low light habitat may have adopted plastic survival strategies required for life in that environment. When transplanted to the shaded treatment, it would likely respond differently to a colony that came from a natal site with higher ambient light levels. This type of phenomenon has been reported previously (Roach and Wulff 1987; Pechenik 2006), for example, Relyea (2002) reciprocally transplanted wood frog tadpoles, *Rana sylvatica*, and found that populations fared better (greater tadpole growth) under conditions similar to their original habitat. The populations of both *P. tuberculosa* and *Z. sansibaricus* from P. Tembakul separate out from their conspecifics in the CDA plots (Fig. 5). This may be due to P. Tembakul being more exposed to ship wakes and associated resuspended sediments—resulting in colonies from there responding differently to the shading treatments at P. Hantu.

Under the right conditions, it is generally agreed that phenotypic plasticity can be adaptive (Via and Lande 1985; Scheiner 1993), but this is often difficult to demonstrate (Todd 2008). Presently, very little is known regarding the functional morphology of zoanthids and it is necessary to look at other colonial cnidarians that have algal symbionts, for example, hard corals (Scleractinia), for clues. Plasticity has been demonstrated in many corals, and light has frequently been considered the main driver (Foster 1979; Dustan 1979; Willis 1985; Gleason 1992). Using a light capture model, Ow and Todd (2010) showed that corallite structure can actively change in response to light availability. For several coral species, lower light conditions are related to more open calical surfaces, exposing a greater amount of tissue to light (Todd et al. 2004a; Klaus et al. 2007). Analogously, zoanthid polyps under the shade treatment had larger oral discs areas that potentially capture more light from a wider range of angles and hence contribute to photosynthesis homoeostasis. The smaller polyps observed in the unshaded colonies are perhaps advantageous in a high light environment where photoinhibition and/or UV damage could occur. Klaus et al. (2007) suggested that the polyps of *Montastrea annularis* (now *Orbicella annularis*) subjected to high light intensities have higher calical relief in order to reduce the amount of tissue exposed and to provide self-shading from excessive UV radiation. Closer examination of the relationship between environment and zoanthid morphology, for instance through modelling (e.g. Ow and Todd 2010), would help identify potential adaptive explanations for the induced changes observed in the present study.

We did not attempt to determine the presence of physiological changes, but it is possible that they could have taken place within colonies. Previous studies have demonstrated the ability of corals and their symbiotic zooxanthellae to adjust their physiology in relation to light (e.g. Jones and Hoegh-Guldberg 2001; Titlyanov et al. 2001; Anthony and Hoegh-Guldberg 2003). For instance, Titlyanov et al. (2001) showed that the coral *Stylophora pistillata* was able to undergo photoacclimation reactions in which zooxanthellae density and chlorophyll content increased in response to low light. Recent work has shown that there is potential for variation in the type of *Symbiodinium* associated with both *P. tuberculosa* (Reimer and Todd 2009) and *Z. sansibaricus* (Reimer et al. 2006e; Kamezaki et al. 2012), even within the same location.

Different *Symbiodinium* types can possess different physiologies (Tchernov et al. 2004), and this may account, to some extent, for among-colony and among-population variations in response to different light regimes. Corals are also able to protect themselves against ultraviolet (UV) radiation through the production of mycosporine-like amino acids (MAAs), which absorb UV (Jokiel 1980; Shick et al. 1996). MAAs are present in zoanthids (Scelfo 1985), but their function, and the mechanism of their production, remains unknown. Corals pay a metabolic cost for the large-scale production of MAAs needed to protect them against constant UV radiation, and it is likely that zoanthids would incur similar costs; thus, this physiological defence is untenable for extended periods of time (Shick et al. 1996; Ow and Todd 2010). In the long term, morphological changes to manipulate light capture should be more adaptive.

The results of the present study demonstrated that both *Z. sansibaricus* and *P. tuberculosa* exhibit phenotypically plastic responses to light treatments. In general, polyps of unshaded colonies were larger than those of shaded colonies. Population × environment interactions showed that populations of both species varied in the magnitude and direction of their responses, suggesting some degree of acclimatization or local adaptation to natal reefs. The presence of non-genetic phenotypic variation in zoanthids may aid the colonization of a broad range of habitats and also enable them to withstand temporal changes in their environment. However, due to their slow growth, longevity, and annual reproductive cycles (Shiroma and Reimer 2010), it is difficult to test, and hence be certain of, the fitness benefits trait plasticity may confer on the two species studied here. We have, nonetheless, provided evidence that environmentally induced changes can contribute to the morphological variation often described in zoanthids.

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