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Palythoa zoanthid 'barrens' in Okinawa: examination of possible environmental causes

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Abstract

Background: Coral reefs are among the most diversified ecosystems in the world, but suffer from anthropogenic and natural disturbances, often causing a shift from coral to algal (or other benthic groups) dominated ecosystems. Linking benthic communities' information with water quality data is urgently needed to understand current and future changes in benthic dominance. This research examined possible environmental causes on the abundance of the zoanthid *Palythoa tuberculosa* on Okinawa Island in southern Japan. Various water parameters (temperature, dissolved oxygen, salinity, pH, particulate organic matter, chlorophyll *a*, NO_2-N, NO_3-N, PO_4-P, NH_4-N, and the distance to the river mouth) were recorded along with benthic community composition at eight locations.

Results: Turf algae, coralline algae, or sand, rubble and rock dominated most locations in this survey. Coral coverage was moderate (10% to 40%). *P. tuberculosa* was generally low in abundance, but common at Mizugama (9% of the benthic community) and Oku (25%). Water parameters varied among sites. Salinity was the only parameter correlated with the abundance of *Palythoa* ($R^2a = 0.47$). *P. tuberculosa* had a positive relationship with the presence of coralline algae, *Pocillopora*, *Goniastrea*, and *Porites*, and had negative correlation with turf algae and other invertebrates.

Conclusions: Likely no single parameter is related to the coverage of *P. tuberculosa* on Okinawa Island. Nutrients were found at low concentrations at the sites, and may explain why there was no strong relationship observed between *P. tuberculosa* and nutrients. Based on these first results, further long-term monitoring combined with the collection of additional environmental data and benthic surveys are needed to better explain the abundance of *P. tuberculosa*. Such data would be particularly helpful to understand how reef organisms will interact with their environment under scenarios of future climate change.

Keywords: Water parameters; Reef benthic community; Phase shift; Zoanthid

Background

Coral reef ecosystems are often called the 'tropical rain forests of the sea' and have the highest biodiversity among ocean ecosystems (Knowlton and Jackson 2008; Bellwood et al. 2004; Hoegh-Guldberg et al. 2007). However, coral reefs are facing severe degradation due to anthropogenic activities and climatic changes. Over-fishing (Hughes et al. 2007), water pollution, extra nutrient input (Szmant 2002), and sedimentation from terrestrial runoff (De'ath and Fabricius 2010) are the main disturbances causing shifts in the dominance of benthic taxa. Over 50% of the world coral reefs are already considered as heavily degraded, and a further 25% will become degraded in the next decade (Wilkinson 2008).

The degradation of water quality plays an important role in the shift from coral to algal (or other alternative taxa) dominated reefs (Bellwood et al. 2004; Knowlton and Jackson 2008). However, its effects on the occurrence of some benthic taxa are still poorly understood. While overfishing has been considered the main factor causing algal over-growth (Done 1992; Hughes et al. 2007), extra nutrient input (Szmant 2002) is also considered as important. The Great Barrier Reef has shown a long-term decline in coral cover in favor of algae correlated to a decline in water quality (De'ath and Fabricius 2010). Similarly, nutrient overload has also been reported to affect negatively coral reef communities from Okinawa (West and van Woesik 2001), Taiwan (Meng et al. 2008), Hong Kong

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(Morton 1994), Reunion Island (Naim 1993), and the Red Sea (Loya 2004), where algae have become dominant at some locations. Sponges are also known to overgrow corals and dominate in locations in the Florida Keys, Belize and Puerto Rico, and in the Pacific Ocean (Rutzler and Muzik 1993; Kelly et al. 2003; Liao et al. 2007; Fujii et al. 2011; Reimer et al. 2011a, b) due to water pollution from human sewage (Ward-Paige et al. 2005), coral disease, and bleaching (Aronson et al. 2002; Weil et al. 2002). Water pollution may be a key factor of corallimorpharian (Anthozoa: Hexacorallia: Corallimorpharia) outbreak in the Red Sea (Chadwick-Furman and Spiegel 2000; Loya 2004; Work et al. 2008). One species of sea anemone (Anthozoa: Hexacorallia: Actiniaria) has been observed replacing the dominant *Acropora* coral community in southern Taiwan, and this was possibly related to chronic terrestrial runoff and tourism pressure combined with the catastrophes of a large typhoon and mass coral bleaching events (Chen and Dai 2004). The factors involved in phase shifts on coral reefs appear to be diverse, but declining water quality is likely to be one of the major driving factors behind these shifts (Chen and Dai 2004). Overall, there is a lack of long-term monitoring of coral reef benthic communities together with water quality and also of precise descriptions of changes in benthic communities correlated with water quality parameters.

Zoanthids (Anthozoa: Hexacorallia: Zoantharia) are common shallow reef benthic organisms, and some zooxanthellate genera such as *Palythoa* and *Zoanthus* are aggressive benthic competitors (Suchanek and Green 1981; Sebens 1982) in specific environmental conditions. In the Pacific, the species *Palythoa tuberculosa* is common in shallow reef areas and is abundant on reef flats and crests in Okinawa (Irei et al. 2011) and in other locations such as in Taiwan (CF Dai and CY Kuo, personal communication). The encrusting form of *P. tuberculosa* combined with up to 65% sand content (Haywick and Mueller 1997) makes it resistant to strong wave energy (Suchanek and Green 1981; Irei et al. 2011). *P. tuberculosa* is an active planktonivore (Fabricius and Metzner 2004), also hosts a generalist *Symbiodinium* type (Reimer et al. 2006; Hibino et al. 2013), and during bleaching events can survive via heterotrophy (Reimer 1971a, b), which allows them to have low mortality during bleaching events (Jimenez 2001), unlike many other bleaching-susceptible anthozoans. Due to a lack of data on the abundance of *P. tuberculosa*, whether this species is naturally abundant or has recently increased in coverage due to induced over-growth by changing environmental conditions is unknown. Studies from Brazil (Costa et al. 2008) demonstrated a positive relationship between *Palythoa* abundance and nutrient-enriched coastal areas. However, no such studies have been conducted in the Pacific.

Okinawa Island is in the Ryukyu Archipelago in southern Japan and is known for its highly diverse coral reefs. However, it has been under increasing anthropogenic threat from coral bleaching (Yamazato 1999; Loya et al. 2001; van Woesik et al. 2004), coastal development, and declining water quality (Roberts et al. 2002; Ramos et al. 2004). At some potentially degraded coral reef locations on Okinawa Island near river mouths, the shallow water communities (1 to 6 m depth) have high coverage of *P. tuberculosa* (Figure 1). This provides an opportunity to examine how the abundance of *P. tuberculosa* is related to environmental parameters in these shallow coral reef waters. To examine this question, water quality parameters and benthic communities were surveyed at eight locations around Okinawa Island.

Methods

Experimental design

The study was carried out along the west and north coasts of Okinawa Island, in the Ryukyu Islands, Japan (Figure 2 and coordinates in Table 1). Okinawa Island is located in the subtropical region, and influenced by the warm Kuroshio Current that contributes to high marine biodiversity (Roberts et al. 2002). Annual water temperatures average from 21°C to 28°C throughout the year (Japan Meteorological Agency 2013). Eight locations from north to south were sampled: Oku, Bise, Manza, Mizugama, Toguchi, Sunabe, Convention Center, and Makiminato. More data about each location's proximity to rivers as well as on nearby coastal land use/conditions are found in Table 1.

Benthic community surveys

This survey primarily focused on the reef crest and reef flat, which are considered as the preferred habitats for

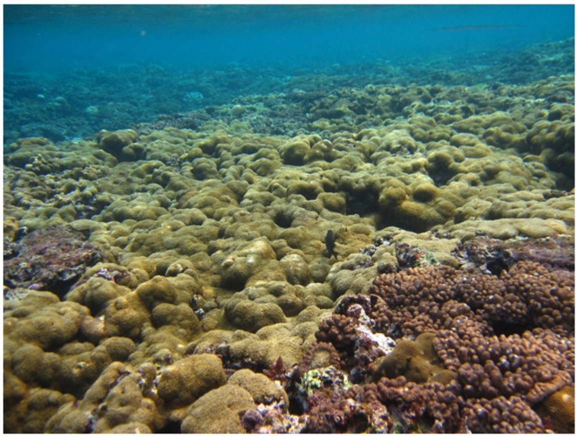

Figure 1 The zoanthid *P. tuberculosa* dominating the benthic substrate at Mizugama, Okinawa Island, Japan. Depth ~ 2 to 3 m.

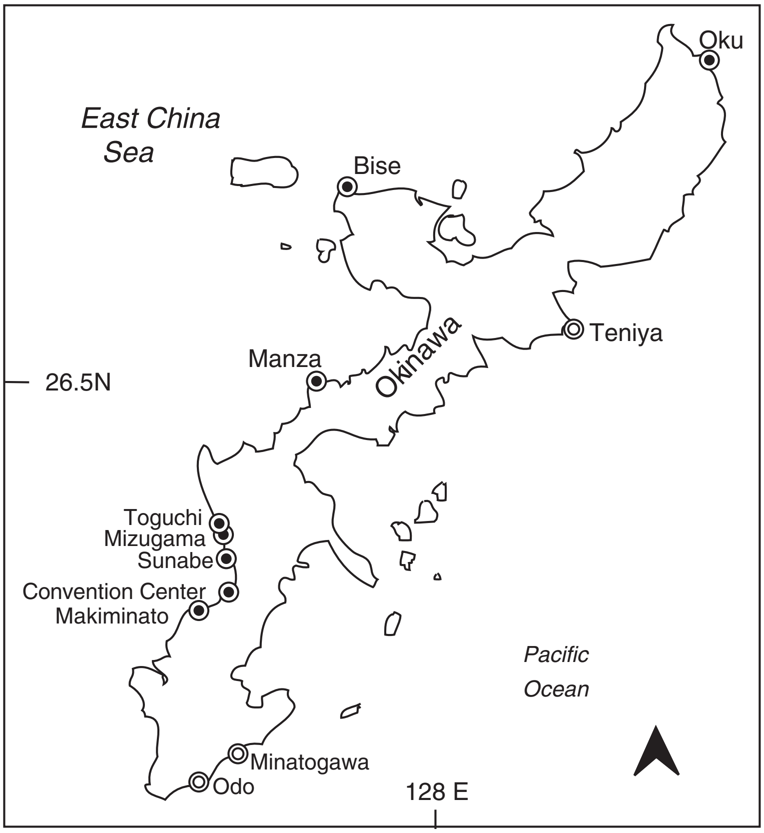

Figure 2 Map of sampling locations around Okinawa Island, Japan. Solid circles signify locations used in all analyses, white circles are additional locations where *P. tuberculosa* are abundant around Okinawa Island.

P. tuberculosa (Irei et al. 2011). Benthic communities were surveyed at each location between July and August 2011 for Bise, Manza, Mizugama, Convention Center, and Makiminato, and May to June 2012 for Oku, Toguchi, and Sunabe. At each location, six 5-m random transect lines were recorded, and serial photos were taken (Canon IXY 920IS; Canon Inc., Tokyo, Japan) along each side of the transect using a 0.5 × 0.5 m quadrat. This study utilized a relatively short (5 m) transect line to avoid topography gaps (e.g., deep spurs and grooves, and channels). The benthic community coverage rates were calculated from 120 random points of each photo using Coral Point Count

Table 1 Geographical coordinates, coastal descriptions, proximal rivers, and distance to river mouths, for eight locations on Okinawa Island, Ryukyu Islands, Japan

Location name	Geographical coordinates	Coastal description	River name and mouth coordinates	Distance to river mouth (m)
Oku	26°50′53.16″N, 128°17′14.45″E	Rice paddy fields nearby	Oku River 26°50′28.92″N, 128°17′31.68″E	1,040
Bise	26°42′39.73″N, 127°52′52.45″E	Upwelling current, near paddy fields to north	Inoha River 26°39′38.94″N, 127°53′49.46″ E	7,025
Manza	26°30′8.99″N, 127°50′33.91″E	Rice paddy fields nearby	River from two dams 26°29′56.45″N, 127°51′ 19.38″E	1,835
Toguchi	26°21′45.92″N, 127°44′12.51″E	Built-up residential area	Hija River 26°21′45.59″N, 127°44′26.98′E	400
Mizugama	26°21′35.17″N, 127°44′18.88″E	Built-up residential area	Hija River 26°21′45.59″N, 127°44′26.98″E	390
Sunabe	26°19′53.01″N, 127°44′31.79″E	Built-up residential area	Small stream 26°20′22.55″N, 127°44′49.74″E	1,125
Convention Center	26°17′4.87″N, 127°44′26.74″E	Taro paddy fields nearby	Small stream from paddy fields	1,355
Makiminato	26°16′30.40″N, 127°42′51.93″E	Adjacent to shrimp aquaculture	Minato-gawa River 26°16′15.88″N, 127°42′ 40.20″E	680

with Excel extensions program (CPCe) (Kohler and Gill 2006). The main benthic groups in this study were turf algae, macroalgae, corals, *P. tuberculosa*, soft corals, coralline algae, other invertebrates, and sand, rubble, and rock (SRR). Combined with detailed information on coral categories, there were 24 groups in total. Anthozoans were identified to family level, except for *P. tuberculosa*. Some corals, beside Fungiidae, Merulinidae, Agariciidae, and Lobophylliidae, were identified to their genus level, namely, *Acropora*, *Galaxea*, *Goniastrea*, *Montipora*, *Pocillopora*, *Porites*, *Psammocora*, *Euphyllia*, *Goniopora*, *Plesiastrea*, *Millepora*, and *Astreopora* following Fukami et al. (2008) and Budd et al. (2012). When individual corals were unable to be identified (e.g., too small), they were designated as 'unknown corals'.

Water sampling and analyses

Water was sampled from Oku, Bise, Manza, Mizugama, Toguchi, Sunabe, Convention Center, and Makiminato at high tide on non-rainy days between the middle of May and the middle of July in 2012. Water temperature was measured using HOBO underwater temperature loggers (UA-002-64, Onset, MA, USA) at five locations (Makiminato, Convention Center, Mizugama, Manza, and Bise) from May 2012 to June 2012, while temperature at the other locations was measured at the time of the sampling using a multi-parameter water quality meter (model WQC-24, DKK-TOA, Tokyo, Japan). Using the same multi-parameter meter, dissolved oxygen (DO), salinity, and pH were measured in parallel. Around 10 L of seawater were sampled at each location, kept in a cooler, and filtered within 1 h through Whatman glass microfiber GF/F filters (pore size = 0.7 μm; Whatman International Ltd., Maidstone, UK). One liter of seawater was filtered for nutrient contents and particulate organic matter (POM); 2 L for chlorophyll *a* (Chl *a*) and 100 ml of the filtered seawater were preserved for nutrient assessment (NO_2-N, NO_3-N, PO_4-P, and NH_4-N). All seawater samples were then preserved at −20°C in the dark until analyses. Chl *a* was extracted using acetone and measured using spectrophotometer following the protocol described by Aminot and Rey (2000). The nutrient levels (NO_2-N, NO_3-N, PO_4-P, and NH_4-N) were quantified using a continuous flow analyzer QuAAtro2-HR (BL-TEC, Osaka, Japan) by following manufacturer's instructions. The Whatman GF/F filters for POM were dried in 80°C and burned at 500°C for 4 h, and the weight was measured before and after burning to calculate POM yield.

Data analyses

In order to satisfy underlying assumptions of statistical analyses and avoid type I and type II errors, the data sets were subjected to transformations prior to multivariate analyses.

The water variables were log-transformed to stabilize their variance, reduce the effects of outliers, and to linearize relationships between variables. Structure and relationships between the environmental parameters (POM, Chl *a*, NO_2-N, NO_3-N, PO_4-P, NH_4-N, salinity, temperature, and DO) among locations were analyzed by performing principal component analysis (PCA) on the transformed data set and by Pearson correlations. To determine if the variation of the environmental parameters are linked to the terrestrial water runoff into the sea, the distance to the closest river mouth were included in the analyses. The statistics of Pearson (r) were tested under 5,000 permutations (Legendre 2005).

The benthic coverage data were subjected to the Hellinger transformation. This method consists of dividing the abundance values by the total abundance in the locations, and then taking the square root of this result. This transformation is recommended for linear ordinations as it reduces the importance of the most common groups and preserves distances between locations in case of absences of some groups at different locations (Rao 1995; Legendre and Gallagher 2001; Legendre and Legendre 2012). To reinforce this last point and avoid disproportionate effects of rare groups in the model, the benthic groups with maximum coverage of less than 5% were removed from analyses. After this, only Merulinidae, *Acropora*, *Galaxea*, *Goniastrea*, *Montipora*, *Pocillopora*, *Porites*, and *Psammocora*, turf algae, macroalgae, *P. tuberculosa*, soft corals, coralline algae, unknown corals, other invertebrates, and SRR remained.

The gradient of benthic composition along the coasts and associations between the benthic groups were analyzed by PCA. For a better view of associations among locations, PCA results were coupled with a clustering analysis following the least-square method of Ward, a hierarchical clustering which can be related to linear methods, such as PCA, in the present case. The number of clusters was determined by Mantel statistics, by calculating the correlation between the original distance matrix and each binary matrix issued from the different levels of the dendrogram. The optimal number of clusters chosen for the final clustering corresponded to the binary matrices presenting the highest correlation with the original distance matrix (Legendre and Legendre 2012). The relationship between *P. tuberculosa* and the benthic groups was also tested by Pearson correlations under 5,000 permutations (Legendre 2005).

To determine which of the environmental parameters interacted with *P. tuberculosa* distribution, a regression analysis was performed on *P. tuberculosa* data with the environmental variables and with the subset of distance to the water networks. Multiple regression was tested by 5,000 permutations. The coefficient of determination R^2 (R^2a) was adjusted by the Ezekiel formula (Ezekiel 1930).

Prior to constrained ordination and regression analyses, covariates exhibiting a high level of colinearity were removed as such variables can cause instability in the model and misinterpretation of the estimators (Zuur et al. 2010). In each model, the colinearity was estimated by compiling the variance inflation factor (VIF) of each variable: the variable exhibiting the highest VIF was dropped, and the VIFs of the remaining variables were compiled again. We repeated the process until all VIFS were under the cutoff threshold of 10 as proposed by Neter et al. (1996).

All statistical analyses were compiled with R software.

Results

Environmental parameters

Detailed information of all water parameters are shown in Table 2. The water temperatures from the 2 months of measurement from five locations showed there were less than 0.5°C differences among all five locations, despite depths being slightly different (Table 2). Salinity, pH, and DO at all locations fluctuated within the natural expected reef environmental ranges (salinity between 25‰ to 42‰ (Coles and Jokiel 1992); pH usually between 8.0 to 8.2, but fluctuating from 7.5 to 8.4 (Meng et al. 2008); DO between 2.1 to 10.8 mg L^{-1} (Kinsey and Kinsey 1967)) despite some locations being close to river mouths. Nutrient concentrations (NO_2-N, NO_3-N, NH_4-N, PO_4-P, and Chl *a*) were all within the level of concentration expected at a general reef area with low nutrient input. The results of the PCA (Figure 3) illustrate the relationships between the variables. The proportions of variation explained by the first two axes were 43.38% and 26.37%, respectively. The first axis displayed a strong gradient of the environmental conditions among the locations: Bise, Manza, Oku, and Sunabe, which are far from river mouths, were grouped on one side of the PCA with high POM, PO_4-P, and pH; while Makiminato, Mizugama, Toguchi, and Convention Center, which are closer to river mouths and had higher NO_3-N, NO_2-N and NH_4-N inputs, were on the other side of the PCA. The second axis separated locations with high temperature (Manza, Makiminato, and Convention Center) and high Chl *a* contents (Toguchi and Sunabe). The Pearson correlation test showed strong correlations between the nutrients and organic matter contents and the distance to the river mouths: the PO_4-P and POM contents increased significantly with the distance to the river mouths ($r = 0.43$, $p < 0.01$ and $r = 0.58$, $p < 0.001$, respectively), while the NO_3-N, NO_2-N and NH_4-N decreased when moving away from the river mouths ($r = -0.86$, $p < 0.001$, $r = -0.84$, p value < 0.001, and $r = -0.76$, $p < 0.001$, respectively). The pH and DO were also positively correlated to the distance to river mouths ($r = 0.67$, $p = 0.001$ and $r = 0.47$, $p < 0.001$, respectively). Neither temperature nor salinity was significantly correlated with the distance to river mouths.

Benthic composition

Benthic composition at most of the locations had high turf or coralline algae coverage ranging between 40% and 70% (Figure 4). For benthic organisms, Mizugama was the only location mainly dominated by hard corals (~40%). Convention Center and Toguchi had moderate soft coral coverage (25% and 15%, respectively), but low hard coral coverage. Other locations had moderate hard coral coverage ranging from 10% to 40%. *P. tuberculosa* coverage was low in Makiminato (<1%), Convention Center (<1%), Sunabe (2%), Toguchi (1%), Manza (1%), and Bise (1 %), but higher in Mizugama and Oku (9% and 25%, respectively). The detailed coral group compositions of locations are shown in Figure 5. Although Makiminato, Sunabe, and Manza had similar amounts of hard coral coverage, their hard coral composition was different. Mizugama was dominated by *Montipora*, whereas Bise and Oku were dominated by *Acropora*. The results of the PCA of the benthic association coupled with cluster analysis are shown in Figure 6. The benthic community was clustered into six large groups, distributed along a north–south gradient along the coast of Okinawa Island (Figure 6). The northern part showed dominance of coralline algae and *P. tuberculosa*. Moving south, locations were gradually dominated by turf algae and coralline algae mixed with some hard coral groups, and finally in SRR, turf algae and some soft coral or macroalgae in the most southern locations. Pearson correlation showed that *P. tuberculosa* had a positive relationship with coralline algae ($r = 0.47$, $p < 0.01$), *Pocillopora* ($r = 0.65$, $p < 0.001$), *Goniastrea* ($r = 0.47$, $p < 0.01$), and *Porites*, ($r = 0.3$, $p < 0.05$), and had negative correlation with turf algae ($r = -0.58$, $p < 0.001$) and other invertebrates ($r = -0.28$, $p = 0.05$), with no significant correlation with other groups.

Analysis of the determinants of the *P. tuberculosa* abundance

The VIFs of the variables NO_3-N, NO_2-N, and DO were superior to the cutoff threshold of 10 and did not show any correlation with the benthic groups. By consequence, these variables were removed prior to the analysis. Multiple regression with the environmental variables on *P. tuberculosa* data showed that salinity was the only sampled variable which contributed significantly to the coefficient of multiple regression ($R^2a = 0.4727$, $p < 0.001$).

Discussion

In the current study, *P. tuberculosa* abundance was found to have a positive correlation with coralline algae and three hard coral groups, *Pocillopora*, *Goniastrea*, and *Porites*, but had a negative correlation with turf algae and ‘other invertebrates’. For anthozoans, coralline algae can be construed as ‘open’ benthic space as they

Table 2 Environmental dataset for eight locations at Okinawa Island, Ryukyu Islands, Japan

	Oku	**Bise**	**Manza**	**Toguchi**	**Mizugama**	**Sunabe**	**Convention Center**	**Makiminato**
Sampling depth (m)	1 ~ 2	1 ~ 2	3 ~ 5	1 ~ 2	1 ~ 2	1 ~ 2	2 ~ 3	3 ~ 6
Temperature (°C)								
May to June 2012 (mean/min/max)	-	24.9/23.2/25.7	25/23.6/25.8	-	25.3/24.3/26.4	-	25.4/24.1/26.2	25.3/24.3/25.9
temperature at the time of sampling	27	27.4	29	25.8	28.6	25.9	28.4	28.5
pH	8.26	8.4	8.21	8.25	8.21	8.22	8.23	8.1
DO (mg L^{-1})	5.35	6.61	4.37	5.23	4.66	6.04	4.41	3.56
Salinity‰	30.1	31.4	30.6	31.1	29.8	31.1	31.7	32.2
POM (mg L^{-1})								
Range	7.97 - 8.45	8.74 - 9.09	8.34 - 8.47	7.13 - 7.34	6.75 - 6.98	7.01 - 7.65	6.9 - 7.2	5.7 - 9.99
Mean + SD	8.167 ± 0.03	8.4 ± 1.67	8.4 ± 0.00	7.22 ± 0.11	6.85 ± 0.00	7.36 ± 0.32	7.2 ± 0.17	7.2 ± 2.16
Chl *a* (μg L^{-1})								
Range	0.08 - 0.12	0.04	0.02 - 0.05	0.24 - 0.28	0.03 - 0.04	0.16 - 0.17	0.04 - 0.07	0.01 - 0.52
Mean + SD	0.1 ± 0.02	0.04 ± 0.00	0.04 ± 0.01	0.27 ± 0.02	0.03 ± 0.01	0.162	0.06 ± 0.01	0.36 ± 0.02
NO_3-N (μM)								
Range	0.26 - 0.31	0.13 - 0.16	0.23 - 0.27	4 - 4.05	1.27- 1.4	0.62 - 0.65	0.67 - 0.69	1.61 - 1.68
Mean + SD	0.28 ± 0.02	0.14 ± 0.02	0.25 ± 0.02	4.02 ± 0.02	1.33 ± 0.06	0.64 ± 0.02	0.68 ± 0.01	1.64 ± 0.03
NO_2-N (μM)								
Range	0.04	0.03 - 0.03	0.03	0.21 - 0.22	0.12 - 0.13	0.07	0.07	0.11
Mean + SD	0.04 ± 0.00	0.03 ± 0.00	0.03 ± 0.00	0.214	0.12 ± 0.00	0.07	0.07 ± 0.00	0.11 ± 0.00
NH_4-N (μM)								
Range	0.58 - 0.93	0.38 - 0.74	0.3 - 0.43	1.56 - 1.64	1.16 - 1.33	0.68 - 0.74	0.87 - 0.92	0.97 - 1.09
Mean + SD	0.74 ± 0.17	0.53 ± 0.17	0.38 ± 0.06	1.6 ± 0.03	1.24 ± 0.08	0.70 ± 0.4	0.90 ± 0.02	1.02 ± 0.05
PO_4-P (μM)								
Range	0.18 - 0.19	0.15 - 0.17	0.17 - 0.18	0.17 - 0.18	0.04 - 0.07	0.13 - 0.16	0.15 - 0.18	0.03 - 0.04
Mean + SD	0.185	0.16 ± 0.01	0.17 ± 0.01	0.18 ± 0.01	0.06 ± 0.15	0.15 ± 0.02	0.16 ± 0.01	0.04 ± 0.00

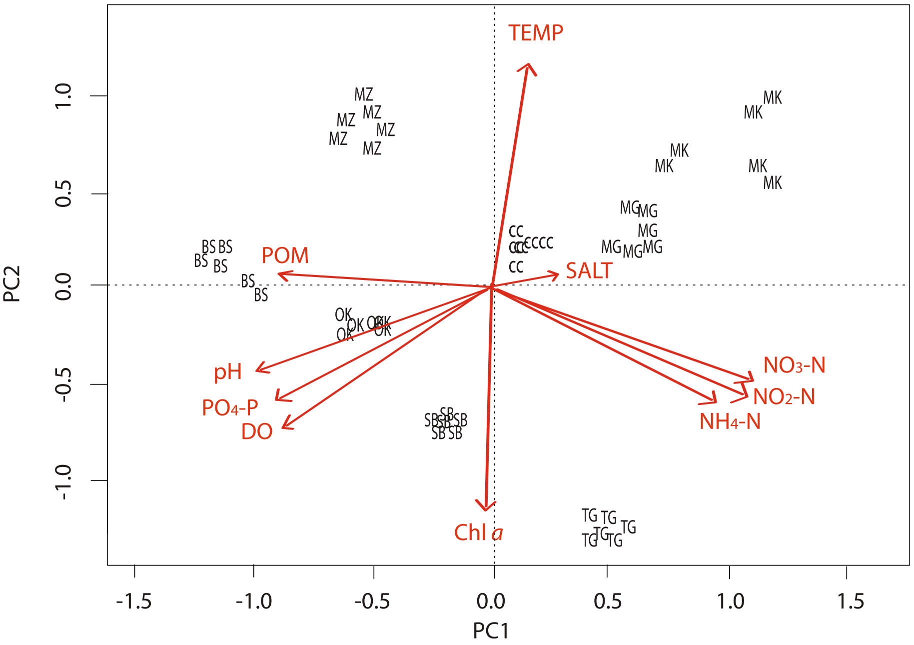

Figure 3 Principal component analysis of environmental data. MK, Makiminato; CC, Convention Center; SB, Sunabe; MG, Mizugama; TG, Toguchi; MZ, Manza; BS, Bise; OK, Oku. PC1 = 43.17%; PC2 = 29.84%.

often settle on top of coralline algae (Heyward and Negri 1999), whereas turf algae compete with other benthic organisms for space. Similar results were also reported in Costa et al. (2008), which implies *Palythoa* may prefer more open reef areas such as outer reef crests (Irei et al. 2011). In this study, other invertebrates consisted mainly of grazing sea urchins and a few sea cucumbers, and these taxa can be expected to have a direct correlation with the abundance of turf algae. The three hard coral groups that had positive correlations with *P. tuberculosa* are commonly found in shallow reefs, and it is therefore difficult to speculate of the nature of the association between *P. tuberculosa* and these groups.

The multiple regression analyses indicated salinity was significantly correlated with the coverage of *P. tuberculosa*, however, the range of the salinity did not fluctuate much among locations. Salinity ranged from 29.8 to 32.2 ‰, levels that are within normal seawater ranges (Coles and Jokiel 1992). Despite some locations in this study being located close to river mouths, salinity did not reach the low levels as seen in Meng et al. (2008), where locations next to stream outlets dropped to 5-15‰. The non-significant correlation observed in this study between the abundance of *P. tuberculosa* and nutrient input may be due to nutrient levels being low compared to Costa et al. (2008). Furthermore, the sampling timing of this study may have influenced the results of water parameters as all the water was sampled during high tide, when runoff of nutrients into the sea maybe more difficult to observe than during low tide. This could explain why the range for salinity was small and no strong relationships were observed between other environmental parameters and *P. tuberculosa* distribution in this study. Previously, *Palythoa* in Brazil was found to be abundant at locations with extra nutrient input (Costa et al. 2008); however, nutrient levels detected by Costa et al. (2008) were much higher than the levels observed in this study. In their survey the total oxidized nitrogen (TON = NO_3^- + NO_2^-) and soluble reactive phosphorus (SRP) from high-nutrient input sites were approximately 2.0 to 2.5 μM and 0.7 to 0.75 μM, respectively. In the current survey, TON ranged from approximately 0.2 to 1.4 μM (except for 4.2 μM in Toguchi), and phosphate (PO_4-P) levels were all lower than 0.18 μM. Chl *a* concentrations were also higher in Costa et al. (2008) (0.8 to 1.3 μg/L) than in our research (0.01 to 0.5 μg/L). Furthermore, Costa et al. (2008) examined reactive silica (DSi), which was not examined in current study, and this may also play an important role in explaining the high coverage of *Palythoa*. However, Costa et al. (2008) only surveyed nutrient-related parameters and did not examine other physical parameters examined in the current study, such as temperature, pH, DO, and salinity. In this study, salinity was the only factor in multiple regression that significantly correlated with *P. tuberculosa*, but other parameters not investigated here (e.g., in Costa et al. 2008) may also be important.

Although the range of salinity in this survey was small, the significant correlation between salinity and *P. tuberculosa* should not be ignored. Low salinity is caused by river, ground water, or precipitation input, which often include nutrients from land (Bell 1992; Costa et al. 2008; Meng et al. 2008). Although there were no significant correlations between salinity and the distance to river

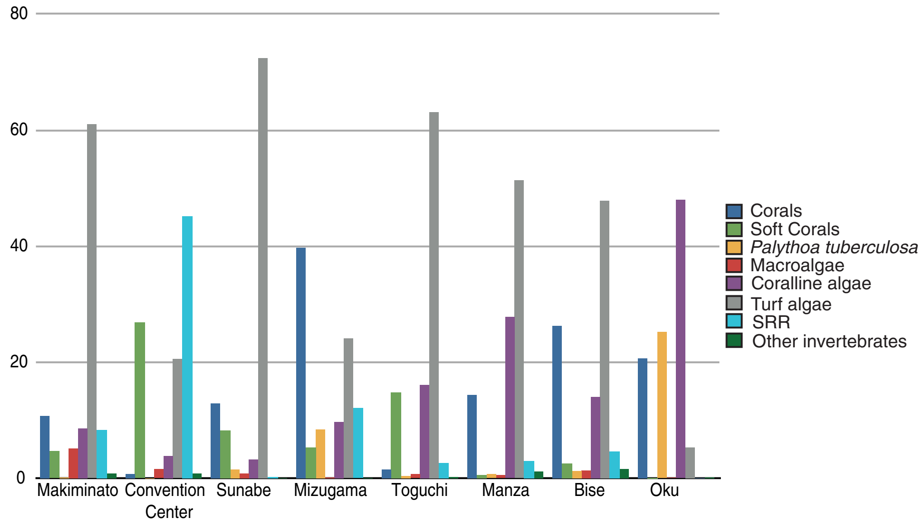

Figure 4 Benthic coverage (%) from eight locations with seven benthic categories. SRR, sand, rubble, and rock.

mouths in this study, NO_3-N, NO_2-N, and NH_4-N had all strong negative correlations with distance to river mouths and were higher in locations close to rivers (Makiminato, Mizugama, Toguchi, and Oku). Despite nutrient input being related to the distance from rivers, some important differences between locations were observed. For example, Toguchi had higher nitrogen levels than Mizugama, although they were the same distance from the closest river. This may be due to the location of the river mouth; the sampling location at Mizugama is located on the southern edge of the river mouth and received less impact than the site at Toguchi, which is located at the northern edge of the same mouth. Sites at Convention Center and Sunabe are not located near rivers yet still exhibited some degree of nutrient input, which may imply terrestrial runoff (Table 2 and Figure 3; also Szmant 2002; Fabricius 2005), as both sites are located adjacent to dense mixed residential/commercial/industrial areas. Around Okinawa Island there are other locations near rivers that experience terrestrial runoff and have been found to have high coverage of *P. tuberculosa* (Irei et al. 2011), particularly two locations in southern Okinawa Island; Minatogawa (216 colonies per 30 m^2) and Odo (155 colonies per 30 m^2). As well, on the east coast of Okinawa Island, the location of Teniya (SYY and JDR, personal observation; Figure 2) was

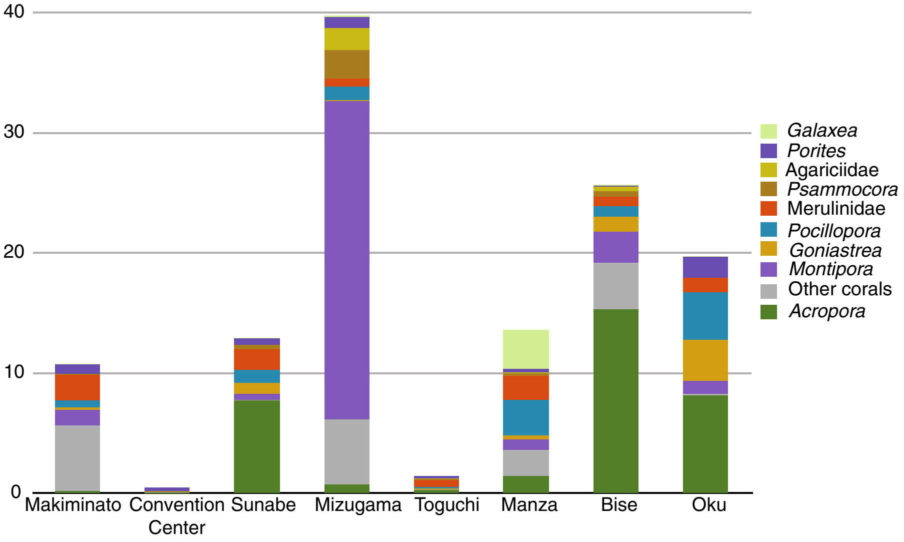

Figure 5 Details of coral coverage from eight locations.

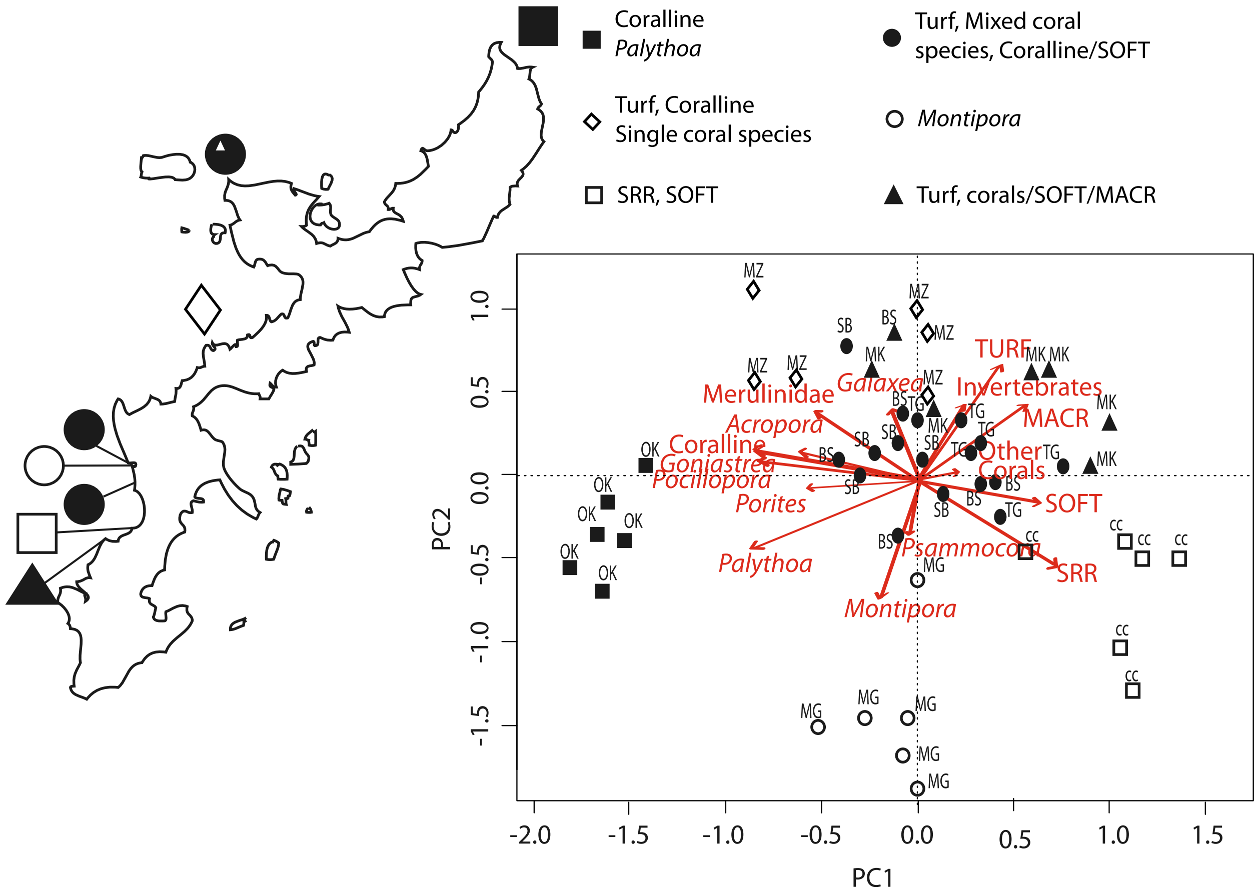

Figure 6 Principal component analysis of benthic community data with cluster group on the map. The legend represents the dominant benthic groups in that cluster (TURF, turf algae; MACR, macroalgae; Coralline, coralline algae; Invertebrates, other invertebrates; SOFT, soft corals; SRR, sand, rubble, and rock; MK, Makiminato; CC, Convention Center; SB, Sunabe; MG, Mizugama; TG, Toguchi; MZ, Manza; BS, Bise; OK, Oku. PC1 = 28.24%; PC2 = 12.74%).

observed to have high *P. tuberculosa* coverage. Minatogawa and Teniya are close to river mouths (Table 2), and Odo has large amounts of freshwater runoff from small creeks (Sakai and Nishihira 1991; Hibino et al. 2013). Rivers and terrestrial runoff both appear to cause extra nutrient input on Okinawa Island reefs; however, input fluctuates throughout the year (Meng et al. 2008). Despite the small range of salinity variation and low correlation levels with other nutrients (perhaps due to the sampling timing), long-term monitoring during low tides should be conducted to further evaluate the role that salinity and nutrient input may play in explaining *P. tuberculosa* abundance.

In Brazil, high coverage of *Palythoa* was observed to be approximately 30% (Costa et al. 2008), while at Oku, in this study, *P. tuberculosa* coverage was approximately 25% despite lower nutrient levels than in the study of Costa et al. (2008). Beside high nutrient concentration and low salinity, other potential factors such as benthic competition or other physical features might also influence the abundance of *Palythoa*. Among the other physical factors, wave energy could be considered as an important factor. *P. tuberculosa* are active planktonivores (Fabricius and Metzner 2004), and their polyp shape which is optimized for feeding under strong water flow (Koehl 1977) makes *Palythoa* a specialist of semi-disturbed reef crests and reef slopes (Suchanek and Green 1981; Irei et al. 2011). Hence, quantifying the wave energy should also be considered in the future research.

Much research has focused on the influence of environmental parameters on hard corals and macroalgae, and there are only a few studies investigating other benthic groups (e.g., West and van Woesik 2001; Costa et al. 2008). Despite the different physiological responses that increased nutrient levels can have on benthic reef organisms, increased nutrient input generally causes coral reef diversity to decrease (Fabricius 2005). Although there were no signs of macroalgal over-growth in this survey, some locations were sub-dominated by soft corals and had low hard coral coverage (Figure 4). Locations to the south of Toguchi had between 5% and 26% soft coral coverage. In other studies soft corals have been observed to increase in abundance with increased nutrient input (McClanahan et al. 2002). West and van Woesik (2001) surveyed how river discharge and human population affected benthic composition in Okinawa, and their survey at Toguchi found that hard coral cover was approximately 11%, soft coral 1%, and *Palythoa* was only 0.1%; while in the current research, *Palythoa* was 0.5%, hard coral cover was only 1.5%, but soft coral had risen to 15%. Therefore, it could be possible that locations such as Makiminato, Sunabe, and Mizugama that do not have high soft coral coverage but suffer from high nutrient input may, in the future, gradually become dominated by soft corals under multiple disturbances. Nevertheless, many soft corals are susceptible to bleaching (Loya et al. 2001; van Woesik et al. 2011), and considering the prediction of continued climate change in the future (Hoegh-Guldberg 1999), soft coral dominance may only be a short-term phenomenon. Such a situation may be the same for *P. tuberculosa*, and instead of becoming dominant under climate change and anthropogenic disturbances, this species may become more abundant in transition stage(s) during phase shifts, particularly with higher fresh water or nutrient input.

Conclusions

It is still difficult to conclude why *P. tuberculosa* is particularly abundant in some locations on Okinawa Island; however, the high correlation with salinity implies extra fresh water input on reefs may be a key factor. Future coral reefs will continue to suffer from high nutrient input, and accompanied by other disturbances such as typhoons or bleaching, reefs may shift to soft coral dominance. Furthermore, if preferable conditions occur, for instance under increased anthropogenic stress, these reefs may shift to aggressive and rapidly growing benthic zoanthids such as *P. tuberculosa*. It is still unknown what the ecological consequences of a phase shift to *P. tuberculosa* dominance would be. Currently, data on reef benthic groups and water quality are lacking in many areas of the Indo-Pacific region. An examination of reefs within predetermined regions combined with more complete environmental data will aid in understanding the dynamics of reef benthic organisms during climate change and anthropogenic disturbances.

Abbreviations

Chl *a*: Chlorophyll *a*; DO: Dissolved oxygen; PCA: Principal component analysis; POM: Particulate organic matter..

Competing interests

The authors declare that there are no competing interests in this research.

Authors' contributions

SYY, CDA, and JDR designed and set up the research. SYY and CDA carried out all the survey and sampling. SYY and CB performed the data analyses. SYY, CB, and JDR wrote the paper. All authors read and approved the final manuscript.

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