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Rapid decline of a relatively high latitude coral assemblage at Weizhou Island, northern South China Sea

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Abstract

"Refuge theory" suggests that global warming would be beneficial to corals in high latitude waters. In theory, then, the Weizhou Island reef (21°00′–21°10′N, 109°00′–109°15′E), which is located in a relatively high latitude area in the northern South China Sea, is a refuge for corals under global warming. Yet, the corals here have degenerated significantly. We investigated the ecological status of the Weizhou Island reef in 2015 and recorded 11 families, 22 genera, and 41 coral species. The mean living coral cover has decreased from ~42% in 1984 to ~10% in 2015 and there are many dead *Acropora* in the study area, especially at the reef flat. Coral assemblage structure has undergone degradation with the dominant group shifting from high complexity branching, foliaceous and massive colonies to a simpler group of massive morphologies. The only sign indicating the corals here benefiting from global warming is the occurrence of a large amount of juvenile *Porites lutea* (31.91% of the total population), which represents the recovery potential of the Weizhou Island reefs. Further analysis concludes that the main reason for the rapid degeneration is escalating anthropogenic impact, such as seawater pollution, unsustainable tourism activities, ongoing overfishing, all of which degrade the local ecological environment. It seems that intensive anthropogenic activities have weakened the "refuge" function significantly. Decreasing living coral cover as well as degraded assemblage structure all suggest that Weizhou Island offers limited potential as refuge habitat for corals in the context of global warming and intensive human activities.

Keywords Coral reef · Relatively high latitude · Refuge · Ecological decline · Anthropogenic activities · South China Sea

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Introduction

Coral assemblage is a collection or gathering of diverse coral species (Adjeroud et al. 2018; Denis et al. 2013). Coral assemblages have declined significantly due to anthropogenic stressors and climate change in the last few decades (Greenstein and Pandolfi 2008; Hughes et al. 2010; Yu 2012). Living coral cover of Caribbean reefs during 1970 and 1983 was about 34.8%, but, according to surveys between 1999 and 2011, dropped to 16.3% (Jackson et al. 2014). Similarly, on the Great Barrier Reef, it declined from 28.0 to 13.8% over 1985–2012 (0.53% year^{-1}), a loss of 50.7% of the initial coral cover (De'ath et al. 2012). On Florida Keys reefs, it decreased from 13 to about 8% between 1996 and 2009 (Ruzicka et al. 2013). Coastal pollution, overfishing, explosions in tourism, disease, global warming, ocean acidification and tropical cyclones were identified to have caused the greatest declines. Coral bleaching has also become widespread and severe (Hoegh-Guldberg 1999; Hughes et al. 2018). There is no doubt that the increasing sea surface temperature (SST) (Hoegh-Guldberg 1999) has already become a major threat to the ongoing existence of coral reefs (Glynn 1996; Hoegh-Guldberg 1999). Many coral reefs—especially those in tropical areas—cannot adapt to this elevated SST, and coral degradation now seems inevitable (Denis et al. 2013; Hoegh-Guldberg 1999).

Under these circumstances, high-latitude reefs have received increasing attention because they are less affected by thermal stress and thus have the potential to act as refuges for corals under global warming (Beger et al. 2014; Glynn 1996). The lower SST of high-latitudes during winter may limit coral recruitment and drive low coral diversity or even cause cold bleaching (Hoegh-Guldberg and Fine 2004). However, global warming alleviates the threat of extreme low temperatures to high-latitude corals to some extent, which should encourage coral reefs' expansion poleward (Denis et al. 2013; Kleypas et al. 1999). This means that some tropical coral species can survive in the high-latitude waters (Halfar et al. 2005). Because of this, high-latitude areas have been viewed as potential refuges for tropical coral reefs (Denis et al. 2013; Halfar et al. 2005; Riegl and Piller 2003). Although the SST of high-latitudes also increases in summer, it is still less than that for lower-latitude counterparts. It is estimated that the Gulf of Aden and southern Red Sea reefs will experience temperatures above 35 °C in 2100, while maximal summer temperatures in the Gulf of Aqaba, northern Red Sea, will still be below 31 °C (Fine et al. 2013). In addition, high-latitude reefs living in cooler water will likely be more resilient to abrupt increases in SST than corals in the lower lattitudes (Halfar et al. 2005; Riegl 2003). They exist in fluctuating environmental conditions and undergo greater temperature changes (Beger et al. 2014), so they may have better adaptability to global climate change (Oliver and Palumbi 2011; Pandolfi et al. 2011; Riegl and Piller 2003). Also, global warming promotes calcification, a limiting factor for reef accretion at high latitudes (Crossland 1984). Hence, global warming can theoretically offer some benefits to high-latitude reefs (Denis et al. 2013; Schleyer et al. 2008). Many high-latitude reefs with less human activities show an optimistic situation and can function as ideal refuge. In Nine-mile Reef (27°24′S), in South Africa, scleractinian cover showed an overall upward trend of 0.26% year^{-1}, from 12% in 1993 and then remaining stable at approximately 18% during 2006–2014 (Porter and Schleyer 2017). At Tatsukushi, Shikoku Island (32°45′N), Japan, coral cover was 60 ± 2% by 2011 (Denis et al. 2013). In Hall Bank (32°02′S), Australia, coral cover was about 52.6% by 2009 (Thomson and Frisch 2010). The high-latitude coral species *Alveopora japonica* has increased its population around Jeju Island (33°20′N), off the southern coast of Korea (Vieira et al. 2016).

Although the expansion of coral reefs from the tropics to the "marginal" subtropics (Greenstein and Pandolfi 2008) provided strong support for the "refuge theory" (Riegl and Piller 2003), global warming adversely affect high-latitude corals with leading to coral bleaching and higher rates of mortality of corals in some extreme anomalous summers (Porter and Schleyer 2017). In Lord Howe Island (33°20′S), Australia, increasing SST led to mass coral bleaching during 2010, with a loss of up to 25% of corals in some part area.The reefs in Houtman Abrolhos Islands (28°17′S and 29°01′S), Australia, and Stetson Bank (28°12′N), Gulf of Mexico also suffered from bleaching events (Abdo et al. 2012; DeBose et al. 2013). In addition, escalating human activities negatively influenced the survival of corals (Hughes et al. 2010). Under these circumstances, more evidence is required to understand the response or suitability (Lybolt et al. 2011) of the high-latitude reefs under natural and anthropogenic stresses. In other words, it is still unclear whether high-latitude areas can really function as suitable habitats for tropical corals.

Weizhou Island, one of the northernmost islands in the South China Sea, has developed coral reefs since the mid-Holocene (~7000 years before present). Theoretically, global warming is beneficial to the accretion and growth of Weizhou Island reef (Yu et al. 2004). Based on instrumental records (Yu et al. 2004), the SST of Weizhou island has been changing almost synchronously with global warming since the 1960s, and the fast warming of SSTs in winter should have already largely reduced the cold stress to local corals.

It is still unknown whether Weizhou Island can provide an ideal refuge for corals of the South China Sea under global warming. We hypothesized that under the degradation of coral reefs around the world, Weizhou Island reef can keep a healthy state and become a refuge where the coral reef had complex assemblages and a high level of coral cover, species richness and recruitment. Therefore, we investigated the ecological status of coral reefs at Weizhou Island to test our hypotheses.

Materials and methods

Study site and local environment

Weizhou Island (21°00′–21°10′N, 109°00′–109°15′E) is 7.5 km long, 5.5 km wide, 26 km^2 in area (Liu et al. 1991) and is 48 km off the southern Chinese mainland coast (Fig. 1). It is the biggest and youngest island in the Beibu Gulf of the South China Sea and was formed by Quaternary basaltic magma(Liu et al. 1991). Weizhou Island is in a relatively high, subtropical latitude where monsoon, ambient sunlight and rainfall are important climatic characteristics. The mean annual air temperature is 22.6 °C; the lowest and highest monthly mean temperatures occur in January (15.3 °C) and July (28.9 °C) respectively; mean annual precipitation is 1380.2 mm (ranging from 635.8 to 2120.7 mm); mean wind speed is 4.8 m/s (ranging from 3.8 to 5.5 m/s); the annual average sea surface temperature is 24.62 °C (ranging from 19 to 30.35 °C); the annual average salinity is 31.9‰; ocean transparency is clear (ranging from 3.0 to 10.0 m); the pH of sea water ranges from 8.0 to 8.23. Moreover, there is cyclonic circulation all the year round. With such climatic attributes and hydrological conditions, it provides an ideal habitat for coral growth and reef accretion, and corals here are mainly distributed in depths less than 10 m.

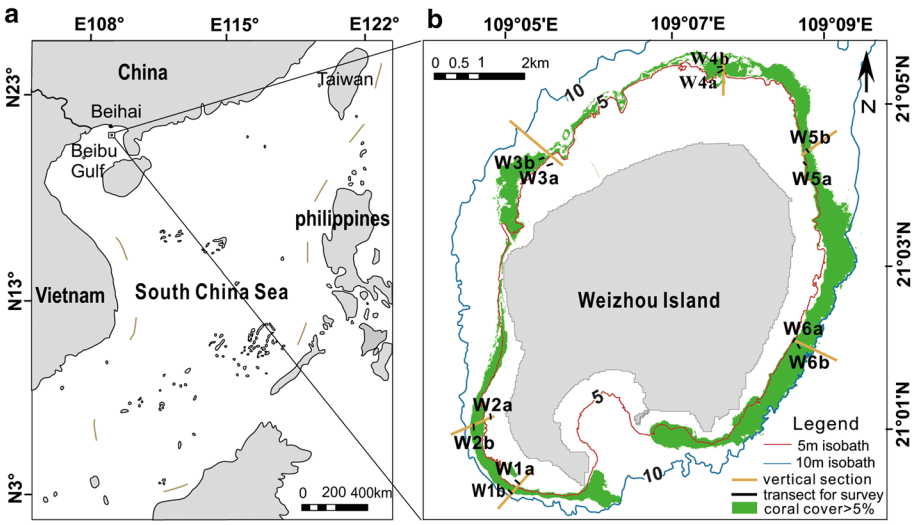

Fig. 1 Locality of Weizhou Island reef and the transects for survey (**a** reef flat, 1 m ≤ depth ≤ 4 m, **b** coral growth zone, 3.5 m ≤ depth ≤ 10 m). Corals were mainly distributed in depths between 3.5 and 10 m

Field surveys

Adopting video transect (Hill and Wilkinson 2004) and photo-quadrat methods (Foster et al. 1991), our field survey was carried out at Weizhou Island reef in 2015. The survey areas of the Weizhou Island reef were concentrated in the southeast, northeast, north, northwest, and southeast of the island in the past decades (Huang et al. 2009; Liang et al. 2010b; Wang et al. 1987). The location of our section was based on the survey in 2007–2008 (Liang et al. 2010b). Based on GPS positioning, six sections (W1–W6) were set up around the island. In each section, two transects with measuring tapes (100 m long) were laid parallel to the shoreline at the reef flat (a: 1 m ≤ depth ≤ 4 m) and the coral growth zone (b: 3.5 m ≤ depth ≤ 10 m) (Fig. 1). An Olympus TG-3 Zoom digital waterproof camera (Olympus Co., Tokyo, Japan) was used to record continuous videos across each transect, and was kept 20 to 30 cm from the measuring tape. The 11 quadrats (1 m × 1 m) were surveyed on each transect, spaced at 10-m intervals and a total of 132 quadrats were established along 12 transects. Four photographs were taken for each quadrat, each occupying one-quarter of the quadrat. We also surveyed the surrounding corals to identify species that may not be recorded. Furthermore, for corals that were difficult to be identified in the field, sampling and classification were carried out in the laboratory.

Data extraction and treatment

Identification of coral species

Species identifications were based on close-up photographs and samples of coral colonies collected from transects, using the taxonomic framework developed by Veron and Zou (Veron 2000; Zou 2001). The number of species (species richness) was determined by

summing up the number of species identified. The potential temporal changes in coral richness were calculated by comparing these coral species that were identified between 2000 and 2015 with those from the studies of the 1960s–1990s. Because of the limited data, the coral species in 1988 were not analyzed.

Analysis of coral cover and size distribution

Living coral cover were based on the line intercept transect procedure (Zhang et al. 2006), which measures the lengths of corals that intercepted a transect line and assesses the percentage cover of the corals by their relative lengths (English et al. 1997). Non-parametric test (Kruskal–Wallis, $p < 0.05$) using SPSS Statistics 19 were performed to detect differences in the coral cover among four surveys between 1984 and 2015.

The maximum diameter of all *P. lutea* in belt transects were recorded according to the measuring tape. Juveniles were defined as colonies < 4 cm in diameter (Edmunds 2000). The size structure of *P. lutea* populations was analyzed with Origin 2017 by calculating descriptive statistics on untransformed data, as follows: mean colony size, smallest and largest colony size (Bak and Meesters 1998). Linear fit were used to investigate relationships between the coral cover and the number of juveniles corals.

Analysis of important values (IVs)

The number of colonies of the coral species i (n_i), the cover of the coral species i (c_i), and the frequency of the coral species i (f_i) in each quadrat were counted respectively. We joined four photographs of each quadrat using Adobe Photoshop software and divided the full image into 10,000 grids. The IVs (GJ 1995) of various corals were calculated to analyze assemblage structure and the dominant species of the coral reef. The species having highest IV was identified as dominant, and the second highest IV was defined as co-dominant species (Melese and Ayele 2017; Toksha et al. 2008). The IVs of coral species is the sum of relative abundance (RA), relative coverage (RC), and relative frequency (RF).

$$\text{Relative abundance } RA_i = n_i / \sum n_i$$

$$\text{Relative coverage } RC_i = c_i / \sum c_i$$

$$\text{Relative frequency } RF_i = f_i / \sum f_i$$

$$\text{Importance value } IV_i = RA_i + RC_i + RF_i$$

Of the 132 quadrats, 63 quadrats were analyzed and there were no corals in other quadrats.

Analysis of the difference and relationship among sections

The species richness and densities of the quadrats were the numbers of coral species and coral colonies in the quadrats respectively. The frequencies and covers of the quadrats were the sum of frequencies of all coral species and the coral covers in the quadrats respectively. With SPSS Statistics 19, differences in the densities and covers among six sections were

examined using a one-way analysis of variance (ANOVA, $p < 0.05$). Kruskal–Wallis test ($p < 0.05$) was performed to detect differences in richness, frequencies and sizes among six sections. Pearson correlation (2-tailed) analysis was used to analyse the relationship among the richness, densities, frequencies, covers.

Analysis of SST

The correlation analysis of year and SST was made with Origin 2017 by unary linear regression equation and analyzed the SST tendency, including the mean yearly average SST (SST_{mean}), mean maximum monthly SST (SST_{max}) and mean minimum monthly SST (SST_{min}).

Data collection and figure generation

The data about coral assemblage in Weizhou Island between 1964 and 2008, including the living coral cover, coral species, dominant species and so on, were extracted from previous studies and reanalyzed (Guangxi Mangrove Research Center 2006; Huang et al. 2009; Huang and Zhang 1987; Liang et al. 2010b; Wang et al. 1991, 1998; Zou et al. 1988), as was the SST data of Weizhou Island between 1990 and 2015 (Chen et al. 2013a; Li et al. 2016; Tang et al. 2010; Yu et al. 2004; Zhou et al. 2010), the nutrient date during 1990–2015 (Han et al. 2015; Li et al. 2016; Qiu et al. 2005; Wei et al. 2005). The data about tourism were provided by Weizhou Island Tourism Management Committee. Figures, including locality of Weizhou Island reef and the transects for survey, changes of dominant coral species at Weizhou Island reef from 1980s–1990s to 2015 were created by CorelDRAW X7. Other figures were generated using Origin 2017.

Results

Species composition and change

A total of 11 families, 22 genera, and 41 coral species were identified at the Weizhou Island reef during our ecological survey in 2015. Numbers of coral species in sections W1–W6 were 19, 13, 12, 10, 17, 7 respectively, with 85.71% of all (28 species) being in W1 and W5 (24 species).

A total of 82 species of coral have been recorded since the 1960s; 32, 30, 17, 64 and 41 species in the 1960s, 1980s, 1990s, 2000s and 2015, respectively (Table 1). Eight species (25% of previous species), four species (13% of previous species) and two species (12% of previous species) identified in the 1960s, 1980s and 1990s respectively were not recorded during researches between 2000 and 2015.

Dominant assemblage

According to IVs, the dominant coral species, genera, and families were confirmed (Table 2). *Porites lutea* (29.5% IV) was the most dominant coral species, and *Favites halicora* (12.1%), *Favites crosslandi* (7.4%) and *Leptastrea purpurea* (6.5%) were co-dominant species. There were 22 species with IVs < 5%, including nine species with values < 1%. At the genus level, *Porites* (29.5%) and *Favites* (24.0%) were the two most dominant genera,

Table 1 Historial records of coral species at Weizhou Island reef

Species	1960s	1980s	1990s	2000s	2015
Poritidae					
Porites					
P. lutea		+	+	+	+
P. andrewsi	*				
P. pukoensis		*			
Goniopora					
G. stutchburyi				+	+
G. duofasciata	+			+	
G. columna		+	+	+	
G. djiboutiensi				+	+
Acroporidae					
Acropora					
A. tumida				+	
A. pulchra	+			+	
A. prostrata			+	+	+
A. millepora	+	+		+	+
A. lutkeni				+	
A. hunilis	+	+	+	+	
A. formosa		+	+	+	
A. cythesea		+	+	+	
A. brueggemanni		+		+	
A. formosa		+		+	
A. corymbosa				+	
A. haimei				+	
A. florida				+	
A. humilis				+	
Montipora					
M. monasteriata	+	+		+	
M. informlis			*		
M. foliosa				+	
M. efflvrescens				+	+
M. digitata				+	
M. hispida	+				+
M. faceolata	*				
M. tuberculosa				+	+
Astreopora					
A. myriophthalma	*				
Anacropora					
A. tapera	*				
Faviidae					
Favia					
F. favus			+	+	+
F. palauensis				+	+
F. speciosa	+	+	+	+	+
F. matthaii	+		+	+	+
F. rotumana		+		+	+

Table 1 (continued)

Species	1960s	1980s	1990s	2000s	2015
Favites					
F. flexuosa				+	+
F. abdita	+	+	+	+	+
F. halicora		+		+	+
F. pentagona				+	+
Platygyra					
P. sinensis			+	+	
P. crosslandi	+			+	+
P. daedalea	+	+		+	+
Goniastrea					
G. aspera		+	*		
G. retiformis		+		+	+
G. yamanarii	+			+	+
Montastrea					
M. curta				+	
Cyphastrea					
C. serailia	+	+		+	+
Plesiatrea					
P. versipora				+	+
Diploastrea					
D. heliopora				+	
Leptastrea					
L. purpurea		+	+	+	+
L. transversa	*				
Echinopora					
E. lamellosa				+	+
E. gemmacea				+	+
Agariciidae					
Pavona					
P. frondifera	+			+	+
P. decussata	+	+	+	+	+
P. varians	*				
P. minuta				+	+
Pachyseris					
P. speciosa				+	
Dendrophylliidae					
Turbinaria					
T. stellulata	+			+	+
T. foliosa				+	
T. elegans	+			+	
T. peltata	+	+		+	+
T. undata	*				
T. itrregularis		*			
T. frondens	+			+	+
T. mesenterina	+	+		+	

Table 1 (continued)

Species	1960s	1980s	1990s	2000s	2015
T. crater				+	
Oculinidae					
Galaxe					
G. fascicoularis	+	+	+	+	+
G. astreata	+	+		+	+
Hydnophora					
H. exesa	+	+		+	+
Merulina					
M. ampliata				+	+
Pectiniidae					
Echinophyllia					
E. aspera				+	+
Fungia					
Podabacia					
P. crustacea	+			+	+
Halomitra					
H. pileus		*			
Mussidae					
Symphyllia					
S. agaricia				+	+
Lobophyllia					
L. hemprichii		+			+
L. corymbosa					+
L. costata			*		
Siderastreidae					
Pseudosiderastrea					
P. tayamai		+			+
Psammocora					
P. contigua		+		+	
P. profundacella	*				
Absent corals	8	4	2		
Total coral species	32	30	17	64	41

+Represents the recorded corals

*Represents the absent corals between 2000 and 2015

and the IVs of the others were all < 10%; including nine genera whose values were < 5% and two genera whose values were < 1%. *Faviidae* (56.2%) was the most dominant family, followed by *Poritidae* (31.8%) and the others were all < 10%.

Coral cover and size distribution of *Porites lutea*

Living corals were mainly distributed at the coral growth zone of six sections, which had an average cover of 10.37 ± 4.2% (ranging from 6.04 to 17.37%) (Table 3). In particular, the northwestern and southwestern coral growth zones reached covers of 17.37%

Table 2 Importance values (IVs) of corals at Weizhou Island reef

(IV rank) Family	(IV rank) Genera	(IV rank) Species	IV	Percentage of IV (%)
(2) Poritidae	(1) *Porites*	(1) *P. lutea*	0.883	29.45
(1) Faviidae	(2) *Favites*	(2) *F. halicora*	0.362	12.06
(1) Faviidae	(4) *Platygyra*	(3) *P. crosslandi*	0.223	7.43
(1) Faviidae	(6) *Leptastrea*	(4) *L. purpurea*	0.194	6.46
(3) Agariciidae	(5) *Pavona*	(5) *P. decussata*	0.179	5.98
(1) Faviidae	(2) *Favites*	(6) *F. pentagona*	0.172	5.73
(1) Faviidae	(2) *Favites*	(7) *F. flexuosa*	0.108	3.60
(1) Faviidae	(3) *Favia*	(8) *F. speciosa*	0.107	3.56
(1) Faviidae	(3) *Favia*	(9) *F. favus*	0.095	3.16
(1) Faviidae	(2) *Favites*	(10) *F. abdita*	0.078	2.61
(1) Faviidae	(7) *Goniastrea*	(11) *G. retiformis*	0.072	2.40
(2) Poritidae	(9) *Goniopora*	(12) *G. djiboutiensi*	0.069	2.30
(4) Oculinidae	(8) *Galaxe*	(13) *G. fascicoularis*	0.068	2.25
(1) Faviidae	(10) *Plesiatrea*	(14) *P. versipora*	0.052	1.73
(1) Faviidae	(11) *Cyphastrea*	(15) *C. serailia*	0.049	1.62
(1) Faviidae	(3) *Favia*	(16) *F. palauensis*	0.043	1.44
(1) Faviidae	(7) *Goniastrea*	(17) *G. yamanarii*	0.040	1.34
(1) Faviidae	(3) *Favia*	(18) *F. matthaii*	0.037	1.23
(1) Faviidae	(13) *Echinopora*	(19) *E. gemmacea*	0.032	1.06
(5) Acroporidae	(12) *Montipora*	(20) *M. efflvrescens*	0.029	0.98
(3) Agariciidae	(5) *Pavona*	(21) *P. frondifera*	0.025	0.83
(6) Dendrophylliidae	(14) *Turbinaria*	(22) *T. frondens*	0.016	0.54
(7) Merulinidae	(15) *Merulina*	(23) *M. ampliata*	0.012	0.40
(1) Faviidae	(3) *Favia*	(24) *F. favus*	0.012	0.40
(4) Oculinidae	(8) *Galaxe*	(25) *G. astreata*	0.011	0.38
(5) Acroporidae	(12) *Montipora*	(26) *M. turgescens*	0.011	0.38
(6) Dendrophylliidae	(14) *Turbinaria*	(27) *T. peltata*	0.011	0.36
(1) Faviidae	(4) *Platygyra*	(28) *P. daedalea*	0.010	0.33

Table 3 Living coral cover (%) and dead Acropora colony cover (%) at the reef flat (a: 1 m ≤ depth ≤ 4 m,) and coral growth zone (b: 3.5 m ≤ depth ≤ 10 m)

Classes	W1	W2	W3	W4	W5	W6	Average ± SD
Living corals							
Reef flat	0.27	5.18	0.29	3.05	1.16	0.06	1.67 ± 2.05
Coral growth zone	15.42	8.67	17.37	7.77	6.04	6.94	10.37 ± 4.79
Dead *Acropora*							
Reef flat	47.04	21.94	37.33	7.84	8.41	29.77	25.39 ± 14.37
Coral growth zone	0.0	0.0	0.0	3.52	0.0	0.0	0.59 ± 1.44

and 15.42% respectively. A large number of dead *Acropora* colonies appeared at the reef flat, and mean dead coral cover was 25.39 ± 14.37%, whilst the living coral cover was just 1.67 ± 2.05% (ranging from 0.06 to 5.18%). The cover of *Porites lutea* occupied 40.9% of the total coral cover, and 73.8% of *Porites lutea* was distributed in the southwest (W1 and W2) of Weizhou Island. There was a significant difference in coral cover among four surveys between 1984 and 2015 (Kruskal–Wallis test, $\chi^2 = 7.89$, $p = 0.048$) and coral cover had declined significantly (Fig. 2).

A total of 890 colonies of *P. lutea* were measured along belt transects in Weizhou Island reef. The maximum diameter ranged in size from 1 to 67 cm with an overall mean diameter of 12.06 ± 11.53 cm (Fig. 3). The number of juveniles was 266 (Table 4), accounting for 31.91% of the total population. Colonies < 8 cm in diameter were occupied 52.13%, and more than 81.01% of the population were < 20 cm. Juvenile corals were mainly distributed in coral growth zones, accounting for 81.95% of the total number of juvenile corals. Size varied significantly among the six sections (Kruskal–Wallis test, $\chi^2 = 34.743$, $p < 0.01$). There was a very significant correlation between cover and the number of juvenile (Fig. 4, $N = 12$, $p < 0.01$).

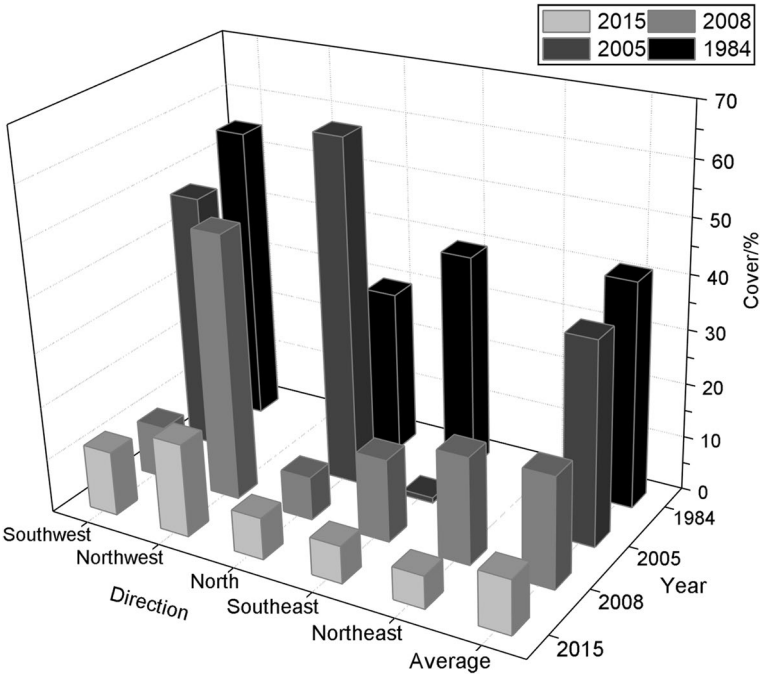

Fig. 2 Living coral cover of Weizhou Island reef between 1984 and 2015. Some positions were excluded from analysis due to lack of repeated investigations. Of the six sections in 2008 and 2015, W1 and W2 were located in the southwest, so the six sections were divided into five sectors. W1 and W2 were replaced by the southwest

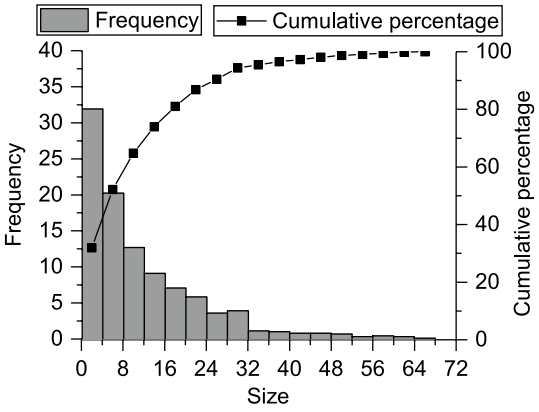

Fig. 3 Size-frequency distribution of *P. lutea* and cumulative frequency

Table 4 The number of juvenile at reef flat and coral growth zone in each transect

Zone	W1	W2	W3	W4	W5	W6	Total	Average ± SD
Reef flat	1	13	3	14	6	11	48	8 ± 5.44
Coral growth zone	53	52	69	20	13	11	218	36.33 ± 24.67

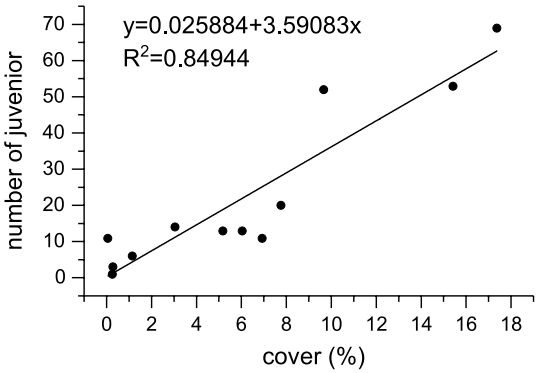

Fig. 4 Correlation between cover and juvenile. There was a very significant correlation between cover and the number of juvenile

Difference and relationship among six sections

Kruskal–Wallis tests showed that there was a significant difference in in richness, frequencies and sizes among six sections ($p<0.01$). Coral covers varied significantly among the six sections (ANOVA, $F=3.52$, $p=0.08$), so were the densities (ANOVA, $F=10.31$, $p<0.01$). There was a very significant correlation among richness, frequencies, densities, covers (Fig. 5, $N=63$, $p<0.01$).

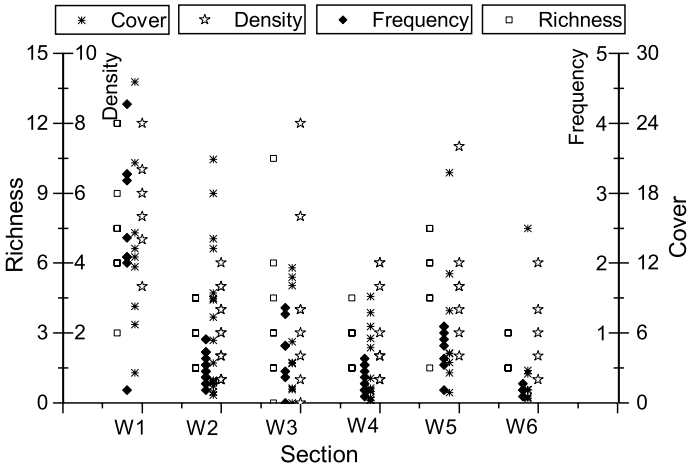

Fig. 5 The richness, frequencies, densities, covers of transects in six section. There was a very significant correlation

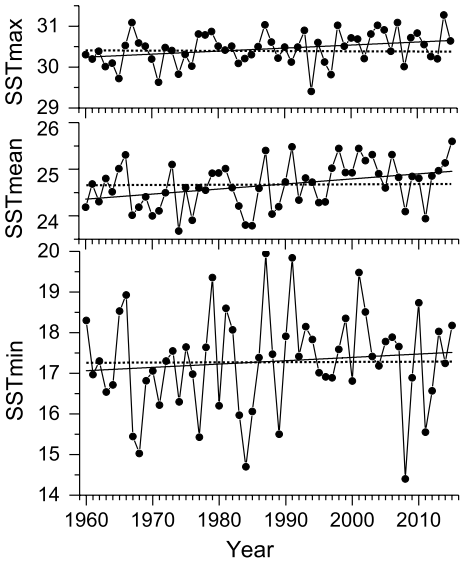

Fig. 6 The SST_{max}, SST_{min} and SST_{mean} of Weizhou Island during 1960–2015 years. Solid and dotted lines show the linear trend and mean value, respectively

SST change

The SST of Weizhou Island changed during 1960–2015 (Fig. 6). Linear models for SST_{min}, SST_{mean} and SST_{max} both showed a positive correlation with year, and the tendency rates were 0.08, 0.07, 0.11 °C/10a respectively. The SST_{mean} was 24.66 ± 0.49 °C. Ranging from 29.41 to 31.28 °C, the SST_{max} was 30.45 ± 0.39 °C. The SST_{min} was 17.29 ± 1.21 °C, ranged from 14.48 to 19.95 °C.

Discussion

Non-uniform spatial distribution

Corals were mainly distributed in the coral growth zones of the southwest (W1 and W2) and northwest (W3) of Weizhou Island, while other sections were relatively few. Correspondingly, the number of juvenile corals in the southeast and northeast was higher than that of other regions. It can be predicted that without major external disturbances, as a large number of juvenile corals grow up, the living corals cover in the southwest and northwest of Weizhou Island will increase gradually. There was a very significant correlation between richness, frequencies, densities, covers, and the parameters of sections W1, W2 and W3 were higher than those of other sections. The corals of Weizhou Island were distributed unevenly in space.

Deterioration of Weizhou Island reef

Temporal variations of coral species

In the past few decades, the coral species recorded in Weizhou Island reef have changed. The change of species composition may be caused by the difference of section layout and incomprehensive sampling, so it could not simply explain the decrease or increase of species in the survey area. Our survey in 2015 identified 11 families, 22 genera, and 41 corals species, 40 of which had been recorded in previous surveys. The earliest introductory ecological investigation at Weizhou Island reef was made by Zou, Zhang et al. in 1964, with 8 families, 22 genera, and 32 species of corals being reported. Afterwards, they recorded 8 families, 23 genera, and 35 species on their second survey in 1984 (Zou et al. 1988). Huang and Zhang reported 10 families, 21 genera, and 45 species in 1987 (Huang and Zhang 1987). In 1998, 19 genera, and 26 species including 9 indeterminate species were reported (Wang et al. 1998). In 2001, Guangxi Oceanic Administration reported 14 genera, 16 species and 4 indeterminate species (Yu et al. 2004). Huang, Ma et al. identified 5 families, 10 genera, and 14 species by coral reef ecological survey in 2005 (Huang et al. 2009). According to data from 2007 to 2008, 10 families, 22 genera, 46 species and 9 indeterminate species were recorded (Liang et al. 2010b). It was noteworthy that the numbers of coral species surveyed in 2001 and 2005 were relatively small. The main reasons were that the former only choosed some representative coral samples, and the latter just identified corals under the sections, which was likely to ignore some corals in other areas. Because of the different investigation purposes, scopes and methods, the numbers reported can't represent the real change, but they provided historic records of coral species. Eight species, four species and two species recorded in the 1960s, the 1980s and the 1990s respectively were not observed between 2000 and 2015. They were unlikely to have been missed during recent surveys because of the more comprehensive methods and more frequent surveys. Thus, it was very likely that those coral species had disappeared from the Weizhou Island reef during sampling intervals. Although there were more species recorded in the twenty-first century than the other three periods, it was unknown whether these new records did not exist in former periods. Perhaps they did not been discovered because of the limitations of the scope and methods of the investigation.

The rapid decline of living coral cover

Mean living coral cover is an important index for assessing the health of a coral reef (Jokiel and Rodgers 2007). There was a significant change in coral cover of Weizhou Island reef between 1984 and 2015 ($p < 0.05$) and it had experienced a rapid deterioration. Our most recent survey indicated the mean living coral cover at the coral growth zone was $10.37 \pm 4.2\%$, ranging between 6.04 and 17.37% (Table 3) and that there were few living corals at the reef flat. The earliest survey about coral cover in Weizhou Island reef was made by Wang, Lv et al. in 1984 and the coral cover was between 20 and 80% (Mo 1989; Wang et al. 1987). Afterwards, they stated in 1991 that living coral cover ranged from 20 to 50–70% in the southeast and that *Acropora* cover was more than 90% at the reef flat of the southwest (Wang et al. 1991). Based on video transect investigation in 2005, the mean living coral cover was ~37.47% (ranging between < 1% and 63.7%), but there were few living corals at the reef flat except in the southwest (Huang et al. 2009). In 2007–2008, 20 investigation transects according to water depth in 2007–2008 showed that the average living coral cover at the coral growth zone was 20.42% (ranging from 8 to 49.2%) (Liang et al. 2010b, 2011). The mean living coral cover decreased from ~42% to just 10% between 1984 and 2015, with an average decrease of 1.03% per year.

It is noteworthy that there existed many dead *Acropora* colonies, particularly in the shallow water, where there was plenty of light and which had been previously suited to *Acropora*. This was especially the case in the southwest and northwest (transects W1a, W3a), where the cover of dead *Acropora* reached 47.04% and 37.33% respectively (Table 3). Furthermore, most dead *Acropora* were corroded and some were smothered by rubbish, epibiota and sediments, which were difficult to remove. The death of *Acropora* and rapid decline in living coral cover both indicate that the prospect of the Weizhou Island reef being a refuge is not optimistic.

The reduction in living coral cover also occurs in other high-latitude or relatively high-latitude areas. The coral cover of Daya Bay (22°31′–22°50′N), China, dropped from 76.6% to just 15.3% during 1983–2008 (Chen et al. 2009). At Wanlitung (22°00′N), in southern Taiwan, China, hard coral cover dropped by 63%, from 47.5% in 1985 to 17.7% in 2010 (Kuo et al. 2012). Florida Keys National Marine Sanctuary (24°20′N–25°20′N) had a mean cover of 5.1% in 1998, but by 2011 average cover of hard corals was only 2.4% (Toth et al. 2014). Total coral cover of Hervey Bay (25°00′S) in Australia was about 45% in 2011—reaching as high as 57% at Big Woody—but there was a 40% reduction post-flood (Butler et al. 2013). Natural disturbances and escalating human impacts have both resulted in the losses of live coral (Darling et al. 2010; Krieger and Chadwick 2013; Lybolt et al. 2011; Medio et al. 1997).

Degradation of assemblage structure

Along with looking at changes in coral cover, quantifying changes in coral taxonomic assemblage structure is also critical for measuring ecosystem state (Darling et al. 2010). Dominated assemblages of Weizhou Island reef have changed in the past few decades (Fig. 7). In the 1980s–1990s, five well-defined zones were apparent: a branching *Acropora* zone (on the northwest), a branching *Acropora* and *Montipora* zone (on the southwest), a foliaceous *Pavona* zone (on the northeast), a massive *Porites*, *Favia*, *Goniastrea*, *Platygyra* zone (on the east and southeast), and a zone with species-diverse assemblages composed

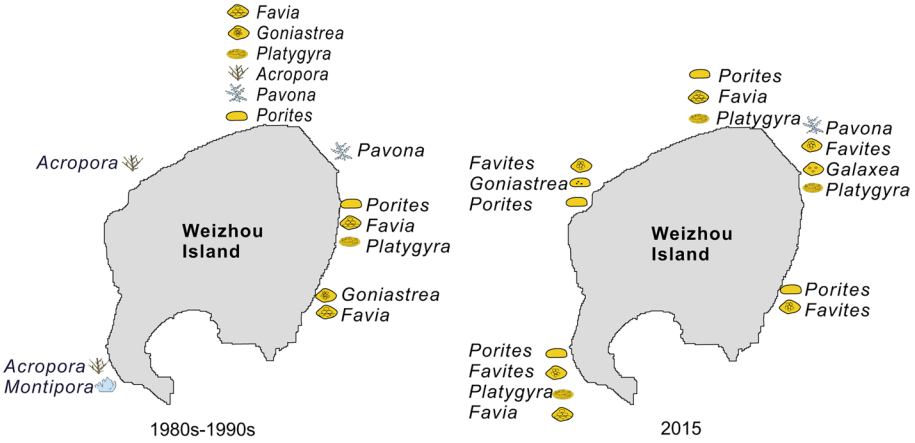

Fig. 7 Changes of dominant coral species at Weizhou Island reef from 1980s to 1990s to 2015

of branching *Acropora*, foliaceous *Pavona*, massive *Porites*, *Favia*, *Goniastrea*, *Platygyra*. In its present degraded state, the former *Acropora* and *Montipora* zones have been replaced by massive clones (*Porites*, *Favites*, *Platygyra*, *Favia*, *Goniastrea*). That is to say, the dominant coral species has shifted from taxa with high structural complexity to taxa that only have disturbance-tolerant massive morphologies.

Acropora has degenerated seriously in recent years and has lost its dominance at the Weizhou Island reef. In 1984, *Acropora* were the dominant species in some areas; branching *Acropora* was particularly abundant at the reef flat of the southwest, with a coral cover of over 90%, whilst the northwest was mainly dominated by procumbent *Acropora* (Wang et al. 1987, 1991). In 2005, *Acropora millepora* prevailed in the southwest with a dominance of 62.3% (Huang et al. 2009). A survey made in 2007–2008 recorded 11 *Acropora* spp., such as *Acropora millepora, Acropora pruinosa, Acropora florida,* but the IV of *Acropora* was only 1.07%, and it was no longer the dominant taxon (Liang et al. 2010b, 2011). Our samples from 2015 showed that *Acropora* existed rarely. Obviously, the *Acropora*-dominated assemblage had disappeared. It is generally accepted that nowadays, massive hermatypic corals—especially Faviidae and Poritidae—occupy the dominate position at Weizhou Island reef (Liang et al. 2010a, 2011).

Studies have shown that environment tolerance varies with coral morphology (Edwards et al. 2001; Marshall and Baird 2000). Branched corals are susceptible to stress while massive and encrusting colonies have a high tolarance (Loya et al. 2001). The main reason is that zooxanthellae density in massive species is higher than in branching species (Li et al. 2008). Corals continuously release mucus and discharge zooxanthellae under stress, which lead to corals bleaching and eventually death (Li et al. 2008). *Porites lutea* with high density of zooxanthellae showed a stronger tolerance to disturbances than *Acropora*. The initial stages of a coral reef are dominated by massive corals like *Porites*, whilst more mature reefs are dominated by *Acropora* (Yu and Zou 1996). Coral assemblages in ideal habitats comprise of both tolerant and sensitive species, whilst those in habitats with detrimental stressors are dominated by disturbance-tolerant coral species (Darling et al. 2010). The dominant assemblage shifting from high complexity branching, foliaceous and massive colonies to a simpler group of massive morphologies indicated that Weizhou Island reef degenerated.

Global warming benefiting to Weizhou Island reef

The SST of Weizhou Island reef increased generally under global warming. The SST_{min} rised slightly faster than SST_{max}, with the tendency rate of 0.08 > 0.07. The SST_{max} ranged from 29.41 to 31.28 °C, a temperature range that corals can roughly adapt to. In other words, the rising SST in summer has put corals on a sensitive edge (Yu et al. 2004), but it has not caused long-term or devastating damage to Weizhou Island corals (Tang et al. 2010). Such as the Maro Reef (25°22′) in the northwestern Hawaiian Islands, although some corals bleached, the reef suffered few substantial long-term impacts from two episodes of coral bleaching (Kenyon et al. 2008).

The SST_{min} in most years dipped below 18 °C, the minimum temperature limit for coral growth. Continuous low temperatures even caused coral cold bleaching; between 1960 and 2010, Weizhou Island reef suffered cold bleaching events five times (Zhou et al. 2010). Low temperatures in winter are restrictive factor for greater accretion of the Weizhou Island reef (Wang et al. 1987; Yu et al. 2004). It is likely that global warming generally benefits to Weizhou Island reef (Yu et al. 2004; Zhou and Li 2014).

Evidence for this can be seen in the size distribution patterns of *P. lutea* at Weizhou Island reef. Juveniles of *P. lutea* accounted for 31.91% of the total population and more than half of the corals are less than 8 cm, which meant that there were a large number of small colonies in Weizhou Island reef. The existence of juveniles *Porites* provides a hopeful sign of potential benefit of global warming. A survey made in 2007–2008 showed that Weizhou Island reef was slowly recovering, and some sections had new recruits (Liang et al. 2010b). Other scholars also observed some newly-grown corals (Shi 2012; Zhou and Li 2014), which demonstrate the recovery potential of coral reefs. All of this suggested that Weizhou Island reef could be a refuge under global warming.

Escalating anthropogenic activities weakening the "refuge" function

From the perspective of latitude, climate and geographical conditions, the natural environment of Weizhou Island is still suitable for coral. However, it has degenerated significantly over past three decades, with coral cover and growth rates continuing to decline (Chen et al. 2013a). The main reason for the rapid degeneration is not climate change but rather anthropogenic activities (Chen et al. 2013c), which may weaken the "refuge" function. In some high-latitude reefs with less anthropogenic disturbance, living coral covers remain stable, such as Tatsukushi, Shikoku Island (32°45′N), Japan (Denis et al. 2013), and Nine-mile Reef (27°24′S), in South Africa even showed an upward trend (Porter and Schleyer 2017).

Seawater pollution

Increased nutrient input is a major factor contributing to the deterioration of water quality, something which is in turn usually associated with coral reef degradation (Fabricius 2005). Elevated nutrient loads affect coral growth and reproduction (Koop et al. 2001), increase disease prevalence and susceptibility to heat stress (McKenzie and Townsend 2007; Thurber et al. 2014), and reduce the temperature threshold of coral bleaching (Wiedenmann et al. 2013). Higher nutrient levels can also stimulate

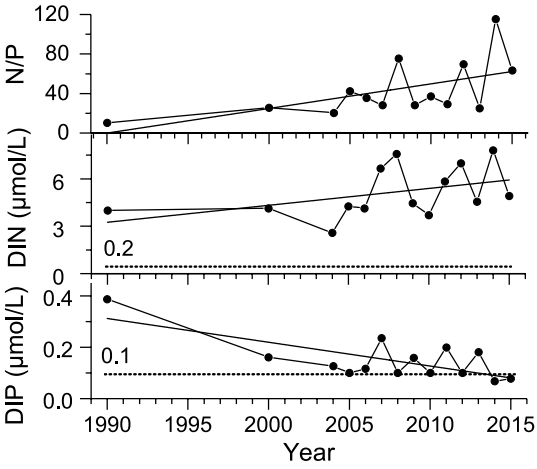

Fig. 8 The DIN, DIP, N/P of Weizhou Island between 1990 and 2015. Solid lines show the linear trend, and dotted lines show the eutrophication threshold levels for DIP and DIN, respectively

algal blooms (Liu et al. 2012), which reduce the growth of corals and inhibit their recruitment (Box and Mumby 2007; Hoegh-Guldberg et al. 2007).

With increasing marine exploitation activities and engineering constructions in Beibu Gulf, the living environment for corals began to deteriorate (Huang et al. 2009). According to previous historic research data (Han et al. 2015; Li et al. 2016; Qiu et al. 2005; Wei et al. 2005), the dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP) and the N/P ratio in Weizhou Island changed in varying degrees (Fig. 8). The concentrations of DIN in Weizhou Island changed greatly and showed an ascending trend (Han et al. 2015). The DIP has changed little in recent years, and the concentration values are all lower than those in 1990. The N/P ratio increased gradually, and the unbalanced ratio can result in detrimental effects such as lowering the threshold of corals to suffer from bleaching and reducing photosynthetic efficiency (Wiedenmann et al. 2013). Levels of both DIN and DIP in the Weizhou Island reef were much higher than those in other areas such as Bahia, Brazil (Costa et al. 2008) and Florida Keys (Thurber et al. 2014). The eutrophication threshold levels of nutrients are 0.1–0.2 μM for DIP and around 1 μM for DIN (Bell 1991, 1992). The nutrients' levels at Weizhou Island—particularly those of DIN—have exceeded this threshold for many years. Indeed, Weizhou Island has experienced several red tides in recent years (Qiu et al. 2005; Zhang et al. 2009) and the intensification of biological erosion is also an important factor leading to the continuous coral degradation (Chen et al. 2013b).

Elevated turbidity can reduce light, thus affecting the photosynthesis of zooxanthellae. Suspended matter and sediments have a negative impact on coral larval survival, settlement rate and growth rate (Jordan et al. 2010; Thurber et al. 2014). Weizhou Island's seawater is turbid. The suspended matter concentration was 30.3 mg/L in 2000 and the mean value of 20.26 mg/L for 2011–2015 (Liang and Peng 2018; Shi 2012; Zhou and Li 2014) far exceeds the third class of suspended matter concentration in coral reefs (> 6 mg/L) (National Marine Environmental Monitoring Center 2005). Wang (2009) found that there was a significant correlation between coral mortality and level of suspended matter. It is likely that the increasing suspended matter has had an adverse effect on the Weizhou Island reef.

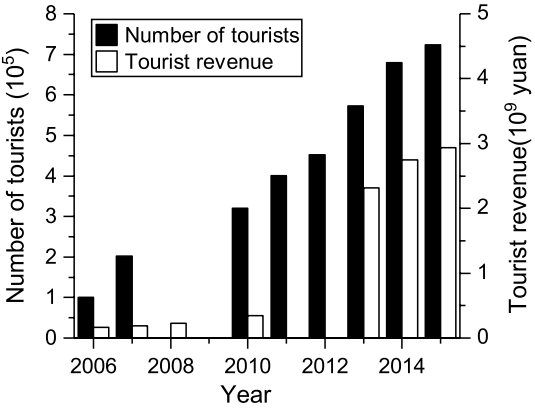

Fig. 9 Tourist numbers and revenues on the Weizhou Island

Unsustainable tourism activities and fishing

Large increases in recreational diving leads to more frequent contact between diving tourists and corals, thus resulting in coral damage (Krieger and Chadwick 2013). Furthermore, increasing numbers of tourists increase the demand for fish, leading to ongoing overfishing and introducing new stresses to coral reef ecosystems (Darling et al. 2010).

Weizhou Island has undergone an economically prosperous period over recent decades: the numbers of tourists increased from 1×10^5 in 2006 to 7.24×10^5 in 2015 (Fig. 9). At the same time, tourism revenue rose from ¥2.58×10^9 to ¥47×10^9 (Fig. 9). Entertainment programs sprung up, including scuba diving and ship sightseeing. At present, there are two diving companies on Weizhou Island, which together own more than 500 sets of imported diving equipment. Also, in order to meet the needs of tourists, a large number of corals were picked for sale as handicrafts. Wang (2009) discovered that the coral species diversity and coral cover of the reef flat in the southwest of Weizhou Island was low due to coral excavation and diving activities. Over-fishing and coral excavation both contribute to coral death (Huang et al. 2009). The offshore fishing capacity around Weizhou Island in 2007 was nearly double that of 1989 (Zhou and Li 2014).

Other coral reefs at relatively high-latitudes are also threatened by human activities. Over exploitation and declining water quality contributed to the recent decline of coral reef in Moreton Bay (Lybolt et al. 2011). Scuba diving and anchoring were the main reasons for coral damage in parts of the Ras Mohammed National Park (Medio et al. 1997). The coral reefs of Kenting National Park face an increasing amount of anthropogenic pressure (Liu et al. 2012). Coral reefs around the world have experienced an unprecedented decline over the past few decades. Weizhou Island reef is near the southern Chinese mainland coast, and suffers exploitative human activities unavoidably. Coastal development, engineering constructions, fisheries, diving, ship sightseeing, the occasional oil leak and other pollutant discharges all bring an excessive burden to the natural environment (Fig. 10) and are leading to the degradation of the Weizhou Island reef.

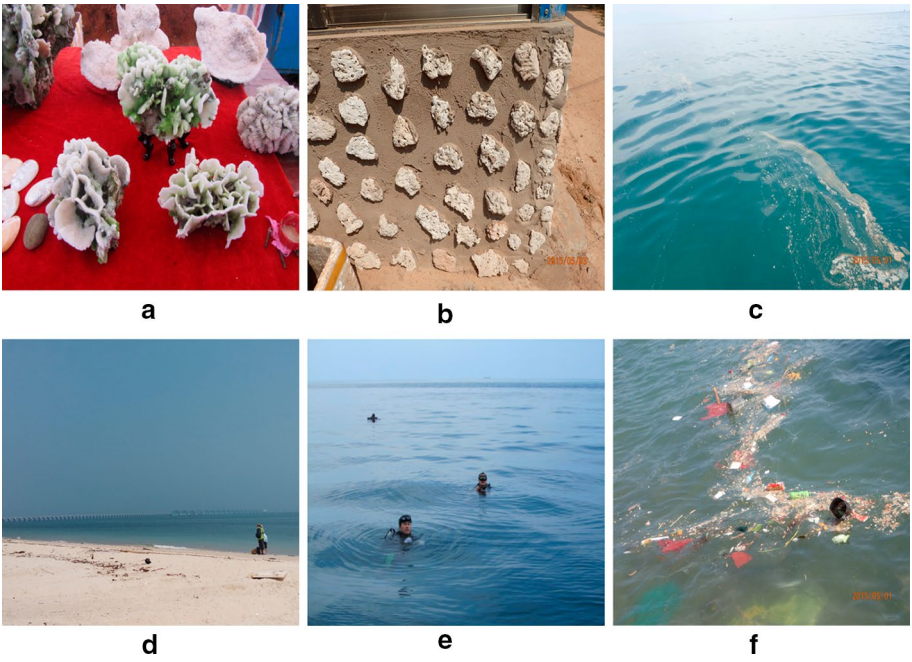

Fig. 10 Examples of various human activities proximal to Weizhou island Reef **a** digging corals for sale; **b** fence decorated with coral rocks; **c** oil polluted seawater; **d** engineering construction, oil–gas pipeline; **e** recreational activities, diving; **f** household garbage. All photos were taken by Xueyong Huang

Conclusion

Weizhou Island reef has degenerated since the 1980s. It suffered massive losses of corals, with mean coral cover decreasing from 41.67% in 1984 to just 10.02% in 2015 and living corals almost disappearing off the reef flat. Fourteen species identified in the 20th century were not recorded during researches between 2000 and 2015 and some species may have disappeared. Although some new species were recorded in twenty-first century, it did not mean that coral diversity had increased because these species may also exist in former periods but were not discovered. Assemblage structure changed from one luxuriant assemblage of species in 1980s to a degraded state where *Porites lutea* has replaced *Acropora* as the most dominant species. The resilience of large numbers of juvenile *Porites lutea* is the only sign suggesting a potential benefit to corals following global warming. Although many high latitude reefs with less anthropogenic stressors show healthy states and can function as refuges, our results suggest that the Weizhou Island reef is undergoing rapid degeneration due to escalating human impacts, which may weaken its "refuge" function. Thus, despite its relatively high latitude, Weizhou Island offers limited potential as refuge habitat for corals in the South China Sea.

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