Benthic community changes following the 2010 Hainan flood: Implications for reef resilience

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Abstract
In the future, coastal coral reefs in Southeast Asia will be exposed to both climate change and more severe and frequent floods associated with heavy rainfall. Floodwaters have caused severe coral mortality in many near-shore coral reefs throughout the world. However, previous studies have largely ignored the effects of floodwaters on macroalgae and calcified algae and the indirect effects on benthic community interactions following flood events. In October 2010, heavy rainfall of more than 1600 mm in 9 days caused the largest flood on record in eastern Hainan Island. Long-term video transects indicate that the floodwater was responsible for severe benthic community mortality in Wenchang, northeast Hainan Island. Mean live coral cover decreased from 15.2% to 9.8% and showed strongest degradation at stations proximal to areas with a high density of aquaculture ponds (i.e. stations 3S–4S decreasing from 15.0% to 0.8%). Branching corals (Acropora and Pocillopora damicornis) were the most sensitive, while massive corals (e.g. Porites, Galaxea, Platygyra and Favia) were most tolerant of floodwaters. Calcified algae were almost completely removed at all stations; coverage decreased from 28.1% to 1.7%, while macroalgae were not influenced by floodwaters. Thus, remnant coral communities that survived the flooding in Wenchang are likely to be subject to increased competition with macroalgae and benefit less from calcified algae promoting juvenile coral recruitment.

Key words: Coral reef; flood; coral mortality; macroalgae; reef resilience; Hainan Island

Introduction
Low salinity has been considered to be one of the most important structuring drivers of near-shore coral growth and reef development (Vaughan 1914; Berkelmans et al. 2012). Strong typhoons and heavy rainfall have caused floodwater to encroach upon coral reefs, leading to significantly decreased salinity in reef waters (Jokiel et al. 1993). Flooding-induced hyposalinity stress, together with sedimentation, nutrient enrichment, light shading and other pollutants, have caused severe coral mortality in many near-shore coral reefs throughout the world (Goreau 1964; Jokiel et al. 1993; van Woesik et al. 1995; Perry 2003; Chavanich et al. 2009; Nakano et al. 2009; Berkelmans et al. 2012). On the Great Barrier Reef, extreme floodwaters associated with tropical cyclone ‘Joy’ in late 1990 and early 1991 caused severe coral mortality at some stations (van Woesik et al. 1995). In Kaneohe Bay, Hawaii, storm floods in 1987 resulted in the complete removal of live coral communities on the reef flat (Jokiel et al. 1993). To date, studies have focused on the direct influence of floodwater on coral communities (e.g. scleractinian corals and soft corals), with less attention paid to other components of the benthic community, such as calcified algae and macroalgae. Furthermore, the indirect influences of floodwater on near-shore coral reef ecosystems (e.g. benthic community interactions) are generally ignored.
Hainan Island is located in the tropical northern periphery of the Indo-Pacific Ocean in the South China Sea (18°10′–20°9′N, 108°37′–111°1′E). The island is 33,210 km² in area, with a coastline of more than 1520 km. Eastern Hainan Island is characterized by a tropical monsoon climate, with the dry season from November to April and the rainy season from May to October. The total annual precipitation of the area is 1500–2000 mm, of which 35–60% is related to typhoon-induced rainfall occurring mainly between July and September (Herbeck et al. 2013). Eastern Hainan Island is affected by northeast wind and waves in winter and southerly wind and waves in summer (Zhang et al. 2006). The coast of eastern Hainan Island is also affected by the seasonal Qiongdong Upwelling, which peaks in summer (e.g. July), bringing lower temperatures (i.e. at least 5°C) and higher salinity (e.g. about 0.3‰ higher) to the coastal waters compared with offshore waters (Jing et al. 2009).

Coral reefs are mainly found shallower than 10 m, covering 14.2% of the coastline of Hainan Island (Zhou 2004). Around the island there have been 110 scleractinian coral species in 34 genera from 13 families recorded (Zou et al. 1975). The coral reefs of Hainan Island are very important for tourism, fisheries and coastal protection (Zhang et al. 2006; Hughes et al. 2013). Additionally, the coral communities of Hainan Island may act as coral larvae pathways from the South China Sea to the coast of mainland China (Wang et al. 2011). However, since the 1970s at least 50% of the fringing reefs of Hainan Island have been destroyed by human activities, including overfishing, land clearing, coral mining, aquaculture expansion and pollution (Zhang et al. 2006; Hughes et al. 2013; Li et al. 2013).

Strong rainfall in October 2010 resulted in severe flooding in eastern Hainan Island, considered to be the largest floods in the past half century (http://www.weather.com.cn/zt/kpzt/480764.shtml; accessed 20 December 2012 (in Chinese)). Wenchang, in northeast Hainan Island, was one of the regions most severely impacted by the flood. The floodwaters had severe negative impacts on the local economy (http://www.weather.com.cn/zt/kpzt/480764.shtml; accessed 20 December 2012 (in Chinese)). More than 1160 villages and 94,340 ha of crops in eastern Hainan Island were flooded, and more than 210,000 people were evacuated. The direct economic loss was estimated at US$180 million. However, the impacts of the floodwaters on near-shore ecosystems (e.g. coral reefs, seagrass bed and mangrove) are unclear.

Figure 1. Locations of 10 stations investigated, shown as closed circles, near Qinglan Harbor in northeast Hainan Island. 1–6: station number, S: shallow back-reef at 3 m depth, D: deep fore-reef at 8 m depth. Closed stars indicate the sites of time-series logging of seawater temperature at 6 m depth.
In September 2009, long-term transects were constructed at 10 stations in the coral reefs of Wenchang (Figure 1). The benthic communities of the reefs were surveyed three times before the 2010 Hainan flood and once after the flood. The aims of this study are: (1) to investigate the benthic community (e.g. scleractinian corals, calcified algae and macroalgae) changes following the 2010 Hainan flood; (2) to determine if the flood was responsible for the severe benthic community mortality in Wenchang; (3) to determine if coral community responses were affected by species composition and proximity to aquaculture ponds (e.g. stations 3S–4S); and (4) to examine the effects of these changes on the community resilience and recovery capacity following the floods. This study provided us with an invaluable chance to examine near-shore benthic community change in response to extreme natural events.

Materials and methods

Study sites

The Wenchang and Wenjiao Rivers enter Bamen Bay with drainage areas of 380.9 km² and 522.0 km², lengths of 37.1 km and 56.0 km and freshwater discharge of 9.1 m³ s⁻¹ and 11.6 m³ s⁻¹, respectively (Liu et al. 2011). In Qinglan Harbor, pollutants from Bamen Bay and passing vessels contribute to the turbid and eutrophic nature of estuaries close to the Qinglan channel outlet (see Figure 1; Liu et al. 2011; Zhou et al. 2012). Study sites are approximately 2.5–10.1 km from the outlet in Wenchang (Figure 1). The distances from the stations to the coastline are 2.3–4 km for stations 3S–4D and 0.4–0.8 km for 5S–6D. South of the harbour outlet, the area is reclaimed land, densely covered with aquaculture ponds. The area to the north of the harbour is densely covered with coconut trees and a few aquaculture ponds (Figure 1).

Rainfall and simulation of freshwater intrusion during the 2010 Hainan flood

Rainfall data for Haikou and Qionghai were obtained from the Climate Center (2010; Figure 2). During the flood, river discharge in Wenchang was estimated as more than 30 times the normal level (Daoru Wang, unpublished data). To evaluate the impact of the flood on coral reefs in Wenchang, freshwater intrusion into the coral reefs (indicated by salinity) was simulated using the Finite Volume Coastal Ocean Model (FVCOM). The FVCOM is a spherical coordinate version of the unstructured-grid finite-volume, three-dimensional (3D) primitive equation coastal ocean model (Chen et al. 2003). In common with other free-surface coastal models, FVCOM uses the modified Mellor and Yamada level 2.5b (MY-2.5) and Smagorinsky turbulence closure schemes as default setups for vertical and horizontal mixing, respectively. There are 7016 nodal points and 13,004 triangular grids. The FVCOM has 10 vertical layers with higher resolution...
near the surface and bottom to better resolve the mixing processes.

Environmental parameters

Environmental parameters are described in detail in Huang et al. (2013). At each station, seawater temperature and salinity were measured in August 2011. Seawater temperature was measured in situ using an AQUAlogger (Aquatec Group, accuracy ± 0.05°C). Salinity was measured using an Orion multiparameter device (Thermo Scientific, accuracy 0.5%). Transparency was measured four times during 2009–2011 using a Secchi disc with 30 cm diameter. Owing to the bad sea conditions experienced during the flood in October 2010, salinity was only measured at stations 1S–2S.

For nutrient analysis, duplicate bottom water samples were collected at each station in May 2010, immediately filtered through pre-weighed glass-fibre filters (Whatman GF/F, 47 mm) and frozen at −20°C. Dissolved inorganic nitrogen (DIN; sum of NH₄, NO₃ and NO₂) was analysed photometrically using an autoanalyser (Model: Skalar SANplus) (Su et al. 2011). To determine the nitrogen sources of the reef waters, the dominant macroalga (*Lobophora variegata* (J.V. Lamouroux) Womersley ex E.C. Oliveira) was collected from each station in August 2010 and their δ¹⁵N analysed using an elemental analyser (ElementarVario EL III) connected to an isotope ratio mass spectrometer (Finnigan Delta Plus XL) (Su et al. 2011). To determine the nitrogen sources of the reef waters, the dominant macroalga (*Lobophora variegata* (J.V. Lamouroux) Womersley ex E.C. Oliveira) was collected from each station in August 2010 and their δ¹⁵N analysed using an elemental analyser (ElementarVario EL III) connected to an isotope ratio mass spectrometer (Finnigan Delta Plus XL). For each station, five samples of *L. variegata* were collected, acidified with HCl (5%) for 30 min, thoroughly washed with filtered seawater to remove sediment particles, and cleaned of epiphytes and possible carbonates. The mixed algal samples were oven-dried at 60°C for 48 h, then ground in an agate mortar, sieved through a 0.6 mm mesh and wrapped in aluminium foil. All samples were measured twice, and the final averaged results are expressed as ‰ relative to atmospheric N₂. The analytical precision was ± 0.3‰ for δ¹⁵N.

A time-series of seawater temperature was obtained from a water temperature meter (JFE, ACTW-USB; accuracy ± 0.02°C) deployed from May to October 2011 in the coral reefs. The meter was deployed at 6 m depth, approximately 14 km northeast of station 6D (Figure 1).

Benthic component survey

Benthic component surveys are described in detail in Li et al. (2013). Briefly, at each station, a 60 m nylon line was fixed parallel to the shoreline at a depth of 3 m or 8 m, and marked with steel stakes at 0, 30 and 60 m. These were used as long-term transect lines for recording changes in the benthic substrate composition at each of the 10 stations (1S–6D). Videos were recorded along each 60 m transect in September 2009, May 2010, August 2010 and August 2011. Using the videos, the benthic community (i.e. scleractinian corals, soft corals, macroalgae, calcified algae, *Millepora*, sponges and zoanthids, dead coral, sand and rock) beneath the transect line was recorded at 10 cm intervals using the linear point intercept method (Nadon & Stirling 2006), yielding 600 points along each transect. The coverage of each benthic component (%) was calculated from the proportion (i.e. total points/600 points). At each station, scleractinian corals were identified to species level and scleractinian coral species richness was estimated. The density of juvenile corals (diameter < 5 cm) was measured using the visual census technique (Edmunds et al. 1998), in at least 32 random quadrats (0.5 m × 0.5 m) along each 60 m transect. Juvenile corals were identified to genus level. Measurements of the density of juvenile coral were conducted three times: in May 2010, August 2010 and August 2011.

Statistical analysis

All community data were tested for the assumptions of normality and homogeneity of variances using Kolmogorov–Smirnov and Levene’s tests, respectively. Paired-sample *t*-tests were used to compare the differences in benthic community data before and after the 2010 Hainan flood. Statistical analysis was carried out using SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, USA).

Analysis of similarities (ANOSIM) permutation tests, based on Bray–Curtis similarities, were used to detect changes in the benthic component composition and coral genera composition following the 2010 Hainan flood (Clarke & Gorley 2006). Non-metric multidimensional scaling (NMDS) was also used to further describe the changes in benthic component composition following the flood (Clarke & Gorley 2006). Similarity percentage analyses (SIMPER) were conducted to assess the respective contributions of benthic substrate types and the coral community to the similarities and dissimilarities in the community structure before and after the flood. All non-parametric analyses were carried out using the software PRIMER v6 (Clarke & Gorley 2006).
Results

Environmental conditions

All environmental parameters are summarized in Table I. During the summer during upwelling in 2011, bottom seawater temperature ranged from 23.9 to 27.6°C and salinity ranged from 33.6 to 34.4 PSU. Transparency was between 1.4 and 7.2 m. Nutrient concentrations ranged from 6.3 to 43.5 µM for DIN and from 0.19 to 0.38 µM for phosphate. In this study, the δ¹⁵N of Lobophora variegata ranged from 5.9–8.0‰. Stations 1S–2S (close to the outlet) were associated with low transparency, high nutrient levels and high δ¹⁵N of L. variegata. The DIN and δ¹⁵N of L. variegata at stations 3S–4S in the south of the harbour outlet were elevated by 2.6–11.4 µM for DIN and 0.4–0.6‰ for macroalgal δ¹⁵N, when compared with values recorded at stations 5S–6S in the north of the harbour outlet.

Rainfall and freshwater intrusion into coral reefs

Between 1 October 2010 and 18 October 2010, strong rainfall lasted for 9 days, with the total rainfall reaching 1221 mm in Haikou and 1176 mm in Qionghai (Figure 2). The exact rainfall level reported by the Wenchang weather station was more than 1600 mm in the 9 days (http://www.weather.com.cn/zt/kpzt/480764.shtml; accessed 20 December 2012 (in Chinese)), which equates to the annual rainfall in previous years. The strong rainfall caused severe flooding in eastern Hainan Island. Field investigations showed that floodwater reduced the surface salinity from 30 to 0 PSU at stations 1S–2S, which was consistent with the simulation result (Figure 3A). Model results also suggested that freshwater swept into coral reefs during the flood and the salinity at back-reef stations 3S–6S declined to 14–16 PSU (Figure 3B).

Benthic community changes following the 2010 Hainan flood

During 2009–2011, 74 scleractinian coral species in 32 genera from 13 families were recorded in Wenchang. Massive coral bleaching was observed at stations 1S–2S, due to hyposalinity stress during the flooding (Figure 4A,B). Community parameters, including live coral cover, coral species richness, juvenile coral density and coverage of calcified algae, all decreased significantly after the flood compared with pre-flood levels (Figure 5). Mean values decreased from 15.2% to 9.8% for live coral cover, from 17.9 to 9.3 no. transect⁻¹ for species richness and from 14.6 to 6.4 no. m⁻² for juvenile coral density. Soft coral coverage declined from 19.1% to 1.7% at station 2S. Calcified algal coverage (mainly composed of Amphipora, Marginisporum, Mesophyllum, Hydroolithon and Neogoniolithon) also declined from 28.1% to 1.7%. However, the coverage of dead coral increased significantly from 21.7% to 56.2%, while coverage of macroalgae (mainly Lobophora variegata) increased from 20.3% to 23.5% (Figure 5). ANO-SIM analysis also confirmed that the benthic community differed following the 2010 Hainan flood when compared with the pre-flood community (Figures 6 and Supplementary material Figure S1; one-way analysis: May 2010 versus August 2011: global R² = 0.387, p < 0.001, dissimilarity 33.49%; August

Table I. Mean values of environmental parameters at the coral reefs of Wenchang.

| Station | Depth (m) | Distance from river outlet (km) | T¹ (°C) | Salinity¹ (PSU) | Trans¹²³ (m) | DIN² (µM) | Phosphate² (µM) | L. variegata³ δ¹⁵N (%) |
|---------|-----------|---------------------------------|---------|----------------|-------------|-----------|----------------|-----------------------|
| 1S      | 3         | 2.8                             | 26.29   | 33.8           | 1.4         | 10.69     | 0.23           | 7.7                   |
| 2S      | 3         | 2.5                             | 26.77   | 33.6           | > 3.0       | 43.54     | 0.21           | 7.3                   |
| 3S      | 3         | 6.4                             | 24.99   | 34.2           |             | 17.72     | 0.30           | 6.4                   |
| 4S      | 3         | 9.8                             | 25.32   | 34.3           |             | 8.87      | 0.20           | 6.5                   |
| 5S      | 3         | 4.7                             | 26.21   | 34             |             | 6.30      | 0.38           | 6.0                   |
| 6S      | 3         | 6.6                             | 27.63   | 33.7           |             | 7.26      | 0.37           | 5.9                   |
| 3D      | 8         | 6.5                             | 24.17   | 34.2           | 6           | 11.07     | 0.19           | 6.6                   |
| 4D      | 8         | 10.1                            | 24.5    | 34.4           | 7.2         | 7.35      | 0.28           | 6.7                   |
| 5D      | 8         | 4.6                             | 23.9    | 34.2           | 5.8         | 6.85      | 0.26           | 6.7                   |
| 6D      | 8         | 6.3                             | 24.6    | 34.1           | 7.2         | 8.39      | 0.35           | 7.0                   |
| 1S–2S   | 3         | 2.7                             | 26.53   | 33.7           | 2.3         | 27.12     | 0.22           | 7.5                   |
| 3S–6S   | 3         | 6.9                             | 26.04   | 34.1           | 10.04       | 0.32      | 6.2            |                       |
| 3D–6D   | 8         | 6.9                             | 24.29   | 34.23          | 6.5         | 8.42      | 0.27           | 6.8                   |

All environmental parameters were measured between one and four times during 2009–2011. ¹August 2011, ²August 2010, ³August 2010. 1S–2S indicates stations 1S and 2S; 3S–6S indicates stations 3S, 4S, 5S, and 6S; 3D–6D indicates stations 3D, 4D, 5D, and 6D. Lobophora variegata: macroalgae. Trans: transparency.
2010 versus August 2011: global $R = 0.517$, $p < 0.001$, dissimilarity 36.3%). Few changes were observed before the flood (May 2010 versus August 2010: global $R = -0.052$, $p = 0.832$, dissimilarity 24.5%, Figure 6).

The changes in coral community following the 2010 Hainan flood were different between stations and between depths. The back-reef stations 3S–6S suffered severe coral mortality and live coral cover decreased from 20.1% to 7.5%. However, live coral cover at the fore-reef stations 3D–6D increased from 14.3% to 14.7%. Stations 3S–4S suffered the most severe coral mortality and live coral cover decreased strikingly from 15.0% to 0.8%. Most coral taxa at these stations were almost completely removed, apart from the genera *Porites*, *Galaxea* and *Platygyra*.

Coral community composition also differed following the 2010 Hainan flood (Supplementary material Table SI; ANOSIM, one-way analysis: August 2010 versus August 2011: global $R = 0.151$, $p < 0.014$, dissimilarity 55.57%). Branching coral coverage, e.g. *Acropora* and *Pocillopora damicornis* (Linnaeus, 1758), decreased significantly while massive corals (e.g. *Porites*, *Galaxea*, *Platygyra* and *Favia*) were less affected (Table SI). The dominant corals changed from *Acropora*, *Montipora*, *Favites* and *Porites* pre-flood, to *Porites*, *Galaxea* and *Montipora* after the flood (Table SI). At stations 3S–6S, coverage decreased from 8.8% to 1.3% for *Acropora* spp. and from 0.8% to 0.1% for *P. damicornis*, while coverage increased from 1.4% to 2.8% for *Porites* spp. and from 1.0% to 1.5% for *Galaxea fascicularis* (Linnaeus, 1767) in response to the flood (Supplementary material Figure S2). At station 2S, soft coral species were also affected by the floods (e.g. coverage of *Sinularia* from 18.6% to 0.7% and *Sarcophyton* from 0.5% to 1%). Changes in coverage and occurrence of juvenile coral species in response to the flooding were consistent with adult coral species (Table SI and Figure S2).

**Discussion**

*Causes of benthic community mortality in Wenchang*

Benthic communities were stable between September 2009 and August 2010 and were severely degraded following the 2010 Hainan flood. During the flood, very low salinity and massive coral bleaching were detected in Wenchang, with model results suggesting severe freshwater intrusion into the coral reefs. Bottom seawater temperature during May–October 2011 did not vary significantly (Supplementary material Figure S3). During the 10 months following the Hainan flood, only one typhoon (Nock-ten) landed in southern Wenchang (about 20 km from station 4S) on 29 July 2011, with a maximum wind speed of 25 m s$^{-1}$ for 6 h (http://agora.ex.nii.ac.jp/digital-typhoon/summary/wnp/s/201108.html.en; accessed 20 December 2012). Thus, the maximum winds for Nock-ten were < 28 m s$^{-1}$ for 12 h, a value inflicting only minor damage on any reef on the Great Barrier Reef (Fabricius et al. 2008) and the typhoon in Wenchang appeared to cause only minor damage on local coral reefs. Moreover, no other extreme events (e.g. dredging and sediment dumping) were observed during that period following the flood in Wenchang. The stable temperature and low wind levels in Wenchang thus suggest that thermal-induced coral bleaching, typhoons and anthropogenic disturbances are not the main factors responsible for the severe benthic community mortality observed, and that the flood was largely to blame.
Changes in the structure of benthic communities

Heavy rainfall over a short time period caused the severe Hainan flood, which resulted in massive coral mortality at back-reef stations. The detrimental effects of floodwater on coral reefs have been reported in many regions around the world, including the Great Barrier Reef (van Woesik et al. 1995; Berkelmans et al. 2012), Kaneohe Bay of Hawaii (Jokiel et al. 1993), Gulf of Thailand Bay (Chavagnich et al. 2009; Nakano et al. 2009) and Mozambique (Perry 2003). The rainfall recorded at Wenchang weather station was much higher than during severe flooding events in Kaneohe Bay (401–777 mm for 5 days; Jokiel et al. 1993) and Mozambique (167–653 mm for one month; Perry 2003); instead, it was similar to levels recorded on the Great Barrier Reef (2000 mm for 15 days; van Woesik et al. 1995).

The response of the benthic community to hyposalinity differed among locations. Although stations 5S–6S were closer to the river mouth, the coral community there suffered less mortality than at 3S–4S, which were further from the river mouth. Stations 3S–4S were located in the leeward area of the river mouth, and their coral communities potentially suffered more severe hyposalinity stress (van Woesik et al. 1995). Moreover, densely packed nearshore aquaculture ponds also appeared to contribute to the severe coral mortality at 3S–4S, owing to the

Figure 4. Benthic communities in Wenchang. Hyposalinity stress caused coral bleaching (A, massive *Porites* and B, *Galaxea fascicularis*) at station 2S during the 2010 Hainan flood (October 2010); community changes at station 3S before (C, August 2010) and after the flood (D, August 2011); partial death of massive *Porites* at station 4S (E, August 2011) and overgrown macroalgae (*Lobophora variegata*) on corals at station 2S (F, August 2011) after the flood.
high levels of sediment, nutrients and other pollutants (e.g. herbicides, pesticides, antibiotics and heavy metals) associated with freshwater discharging into the coral reefs during the flood. Although direct measurements of pollutants during the flood are lacking, our environmental data and previous studies all suggest that stations 3S–4S suffered more severe eutrophication and organic matter enrichment from the coastal aquaculture ponds compared with stations 5S–6S (Herbeck et al. 2013; Li et al. unpublished data). The corals were most likely affected by combined stressors such as low salinity, high sedimentation, low light, and high nutrient levels (Fabricius et al. 2007; Humphrey et al. 2008; Lirman & Manzello 2009).

Calcified algae coverage significantly decreased after the Hainan flood while macroalgae were not influenced by hyposalinity stress. These results were consistent with other studies (van Woesik 1991; Pereira & Goncalves 2000). The 2000 southern Mozambique floods caused severe coral mortality, where the coverage of calcified algae decreased by 85.1% and coverage of macroalgae and turf algae significantly increased by 80.4% and 164.4%, respectively (Pereira & Goncalves 2000). Although the extreme floodwaters in late 1990 and early 1991 caused severe coral mortality on the Great Barrier Reef, the abundance of macroalgae (Lobophora variegata, also the dominant macroalga in Wenchang) did not appear to be affected by low salinities (van Woesik 1991). Some macroalgae can tolerate salinities of 7–52 PSU without any physiological stress (Kirst 1990), suggesting greater osmotic adaptation. However, the reason for the susceptibility of calcified algae to floodwater was unclear. Calcified algae are also very sensitive to sedimentation and ocean acidification (Fabricius 2005; Anthony et al. 2008). Herbicides (e.g. diuron) in floodwaters also pose a risk to calcified algae, and the effect of these herbicides is compounded by sedimentation stress (Harrington et al. 2005).

‘Winner’ and ‘loser’ corals
Response to hyposalinity differs among coral species. In this study, branching corals were the most sensitive while massive corals were the most tolerant. The results were confirmed by previous field and physiology studies (Jokiel et al. 1993; van Woesik et al. 1995; Perry 2003; Li et al. 2009; Nakano et al. 2009; True 2012). On the Great Barrier Reef, mortality was
highest in shallow Acropora spp. and pocilloporids (i.e. Pocillopora damicornis and Seriatopora hystrix Dana, 1846); conversely, faviids were the most tolerant of flood conditions (van Woesik et al. 1995). In Kaneohe Bay, P. damicornis was the most sensitive to lowered salinity, while Porites compressa Dana, 1846 was the most flood-resistant of the scleractinians and survived in areas where all other coral species had been eliminated by flood conditions (Jokiel et al. 1993). Berkelmans et al. (2012) estimated the critical salinity threshold for Acropora spp. ranging between 28 PSU and 22 PSU for exposures of 16 and 3 days’ duration, respectively, which are apparently higher than the threshold for most reef corals (15–20 PSU; Edmondson 1928; Coles & Jokiel 1992).

Responses of juvenile coral species to floodwater were consistent with observations on adult corals. Larvae of Acropora were the most sensitive to hyposaline conditions and did not achieve full development when exposed to low salinity conditions (e.g. 28 PSU) for 4 days (True 2012). However, larvae of massive corals (e.g. Platygyra) were the most tolerant of salinity stress, but settled larvae at low salinities were observed to be lower, smaller and paler than the controls (True 2012). In comparison with adult corals (e.g. the salinity threshold for Acropora at 28 PSU: larvae for < 4 days and adult for 16 days; Berkelmans et al. 2012; True 2012), juveniles should be more sensitive and the actual salinity threshold is higher for juveniles.

Overall, the inter-species variability suggests that branching corals (e.g. Acropora and Pocillopora) may be the ‘losers’, and massive corals (e.g. Porites, Galaxea, Platygyra and Favia) may be the ‘winners’ in response to flooding, with the latter exhibiting greater resistance and resilience to more frequent disturbances in the future.

Implications for reef resilience
In 2010 before the Hainan flood, our previous study showed that two biological processes controlled the distribution of coral communities in Wenchang (Li et al. unpublished data). Overgrowing macroalgae negatively affected coral communities, while abundant calcified algae were beneficial to coral communities by promoting juvenile coral recruitment. Although at some stations the benthic community had already shifted to communities dominated by macroalgae (Wang 2001; Li et al. unpublished data), the benthic community was stable in Wenchang between 2009 and 2010 (Figures 6 and 7) and in Bangtang village of Wenchang between 2005 and 2010 (Figure 7). Following the 2010 Hainan flood, the differing responses of calcified algae and macroalgae to floodwater may have significantly influenced the benthic community interactions in Wenchang. For example, there will have been a reduction in the positive effect of calcified algae on coral recruitment. However, the remnant coral community that survived the flooding in Wenchang will have been subject to greater competition from macroalgae, especially Lobophora variegata (Figure 4F). This will most likely create a benthic community that is dominated by macroalgae, with reduced coral recovery after the flood event.

Benthic communities in eastern Hainan Island have changed greatly in the past few decades. In 1980, the benthic communities were mainly composed of scleractinian corals and calcified algae (Wang 2001). However, the extent of macroalgal cover varied temporally owing to strong herbivory (Wang 2001). Benthic community composition was similar to the pristine reefs of the northern Line Islands (Sandin et al. 2008). In Wenchang, live coral cover declined dramatically from about 50–60% in 1980 to 18.3% in 2009, 15.2% in 2010 and 9.8% in 2011 (Figure 7). Macroalgal cover has increased greatly, as a result of overfishing and nutrient enrichment (Li et al. unpublished data). Based on the recovery rates observed following the two flood events in Kaneohe Bay, it is thought that coral reefs can recover quickly from natural disturbances, but not in polluted conditions (Jokiel et al. 1993). A field manipulation experiment on the Great Barrier Reef demonstrated that drastic reductions in fish grazing can cause harmful macroalgal blooms and reduce the recovery of corals following bleaching-induced
mortality (Hughes et al. 2007). Thus, following the flood, reef resilience and potential recovery will be greatly undermined by the overgrowth of macroalgae due to nutrient enrichment and overfishing.

In conclusion, the 2010 Hainan flood resulted in severe benthic community mortality in Wenchang. Live coral cover, species richness, juvenile coral density and coverage of calcified algae all declined significantly. However, macroalgal cover increased slightly following the flood, and thus, the remnant coral communities may be exposed to greater competition from macroalgae. In the future, monsoon rainfall in Southeast Asia will become more intense as a result of climate change (Cruz et al. 2007). In eastern Hainan Island, heavy rainfall was also associated with the El Niño–Southern Oscillation (Peng et al. 2002). This means that coastal coral reefs will be exposed to more severe and frequent flood events in the future (Cruz et al. 2007). Thus, management actions, such as recovering herbivory (i.e. herbivorous fish and sea urchins) by building no-take zones and controlling pollutant flux to coral reefs (e.g. nutrient, sediment, herbicides, pesticides, antibiotics and heavy metals) by catchment management (Hughes et al. 2007), have to be implemented to improve reef resilience and increase the chances of recovery.

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