Impacts of multiple disturbances on coral communities at Ishigaki Island, Okinawa, Japan, during a 15 year survey

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ABSTRACT: Coral reefs have been threatened by various human and natural environmental disturbances, especially by widespread water temperature increases in 1997/1998. To understand the recovery of coral communities and shifts in their species compositions, long-term monitoring at the same location is important. Previously, we reported changes in the dominant taxa in a coral community before and after bleaching in 1998 at Shiraho Reef in the southern Ryukyus, Japan. In the present study, we continued monitoring the site for 15 yr to quantify how the coral community changed temporally and spatially. We used transect surveys and time-series aerial photographs and analysed the data with reference to seawater temperature and typhoon records. Net coral area along the transect lines increased from 1998 to 2003, but then decreased by 2008 mostly due to a decline in branching *Montipora* spp. The resulting net coral area was lower in 2012 than it was before the 1998 bleaching event. Aerial photographs also showed that the coral area at Shiraho Reef was similar between 1995 and 2000, but declined afterward. This decrease resulted from multiple disturbances, including bleaching events in 1998 and 2007, physical damage by 5 consecutive strong typhoons and likely inputs of sediments from heavy rain. Coral taxa reacted differently to the environmental stresses. The main change observed was a shift in the dominant taxa from branching *Montipora* and *Acropora* to *Heliopora coerulea* and massive and branching *Porites*. Those species have persisted due to high recruitment rates in *H. coerulea* and/or their tolerance to disturbances such as high thermal stresses, sedimentation and physical damage by typhoons.

KEY WORDS: Coral reef · Disturbances · Long-term changes

INTRODUCTION

Coral reefs have been negatively affected by a variety of environmental changes in recent decades. These changes include increasing seawater temperatures that have led to bleaching events (Hoegh-Guldberg 1999, Hughes et al. 2003, Pandolfi et al. 2003), ocean acidification (Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011), pollution including sedimentation and eutrophication (Tomascik & Sander 1985, Fabricius 2005), diseases (Bellwood et al. 2004, Sutherland et al. 2004, Harvell et al. 2007), outbreaks of coral predators such as *Acanthaster planci* (Fabricius et al. 2010) and increasing competition with algae as a consequence of overfishing (Bellwood et al. 2004, Hughes et al. 2007). In addition to these anthropogenically driven disturbances, natural disturbances such as tropical storms (hurricanes, typhoons and cyclones; Knowlton et al. 1981, Fabricius et al. 2008) affect coral reefs. For example, the global

coral bleaching events of 1997 and 1998 affected many coral reefs, leading to a substantial decrease in the percent area of coverage of live corals (Hoegh-Guldberg 1999). The frequency and scale of disturbances are shifting reef communities from coral-dominated to algal-dominated states (Hughes 1994, Bellwood et al. 2004, Hughes et al. 2010), although some communities do not follow this trend (Bruno et al. 2009, Cabaitan et al. 2012).

To understand the impacts of these disturbances on coral communities, long-term monitoring at the same location is a priority. Studies on coral community changes have shown that the rate of recovery in coral communities depends on the location or the coral species (Connell et al. 1997, Loya et al. 2001, Edmunds 2002, Baker et al. 2008, van Woesik et al. 2011, De'ath et al. 2012, Gilmour et al. 2013). Long-term monitoring also allows us to integrate the impacts of multiple stressors. For example, a decadal time scale shift in the structure of coral assemblages has been observed in the Great Barrier Reef and Moorea, French Polynesia, due to bleaching events, outbreaks of *A. planci* and tropical storms (Wakeford et al. 2008, Adjeroud et al. 2009, Pratchett et al. 2011). The least susceptible taxa are thermally tolerant species (e.g. *Porites* spp.), remnant survivors that rapidly re-grow (e.g. *Montipora* spp.) and species with high recruitment (e.g. *Acropora* spp.; van Woesik et al. 2011, Gilmour et al. 2013). These studies, however, have focused mainly on coral reefs less subject to direct local human activities that can result in high sedimentation rates and eutrophication.

In the Ryukyu Islands, Japan, the 1998 bleaching event caused significant damage to coral reefs (Loya et al. 2001, Kayanne et al. 2002). Previously, we reported changes in the coral community of Shiraho Reef, Ishigaki Island, over a 2 yr period (1998 to 2000) based on surveys of permanent transects conducted before and after the bleaching event (Kayanne et al. 2002). After a strong decrease in coral species and percent coverage due to bleaching, the community recovered rapidly. The recovery was due especially to increases in some large patches of branching *Montipora* spp., which had decreased by 41% but recovered to 90% by 2000 compared to May 1998 (Kayanne et al. 2002). However, other environmental factors also influence Shiraho Reef, including the accumulation of red soil and high nutrient inputs resulting from land development since 1972, which has led to increases in the incidence of seagrass beds along the shore line (Hasegawa 2011). In addition, a severe bleaching event in 2007 (Dadhich et al. 2012) and several typhoons have affected Shiraho Reef.

In the present study, we examined the coral community at Shiraho Reef using permanent transects over a 15 yr period (1998–2012). Our goal was to determine the long-term effects of natural and anthropogenic influences on coral community structure. Included in our analysis are spatial changes in the total coral area based on a time-series of aerial photographs and discussion of the relative importance of disturbances on Shiraho Reef based on line transect data.

MATERIALS AND METHODS

The study site was located on the Shiraho Reef flat at Ishigaki Island, southwestern Japan (Fig. 1A, 24° 21′ 50″ N, 124° 15′ 17″ E; Kayanne et al. 2002). Between 200 and 400 m from the shoreline, the water depth was about 2 m, and shallowed to <50 cm beyond 600 m from the shoreline (Transect S6 in Fig. 1B; Kayanne et al. 2002). Among the 6 dominant coral taxa (*Acropora* spp., *Montipora* spp., branching *Porites* spp., massive *Porites* spp., *Pavona* spp. and the blue coral *Heliopora coerulea*), massive *Porites* spp. were distributed in seagrass beds (100 to 200 m from the shoreline), whereas the others corals were typically found beyond 400–500 m from the shoreline and were distributed on the reef pavement close to the reef crest. Five belt transects (1 m width) were set from the shoreline to the crest (750–800 m) to observe coral zonation in the reef (Transects N12, N6, CL, S6 and S12 in Fig. 1B; Kayanne et al. 2002). Each taxon was visually recorded as 0% cover, 1% cover and subsequently 5% cover intervals (e.g. where 10% means cover of 7.5 to <12.5%, 15% means from 12.5 to <17.5%, etc.) every 10 m along the transect over a width of 1 m. We examined the percentage cover 8 times between 2001 and 2012 (17 to 19 October 2001; 5 to 7 July 2003; 25 to 27 July 2005; 4 to 5 August 2008; 22 to 24 August 2009; 28 to 31 August 2010; 18 to 20 October 2011; 31 October to 2 November 2012) in addition to the previous surveys conducted between 1998 and 2000 (8 times; Kayanne et al. 2002). The net coral area was derived from the percentage cover on each transect as follows:

$$\sum (10 \text{ m}^2 \times (\% \text{ cover})/100) \qquad (1)$$

After summation of the net area for all corals in each transect, the relative cover was normalised to that of May 1998 (= 100%). A general linear model (GLM) 1-way ANOVA was used to detect differences in net coral area between years (May 1998, 2003, 2008, 2010) within each taxon, except *Pavona*, which was only observed at Transects N6 and N12. Years
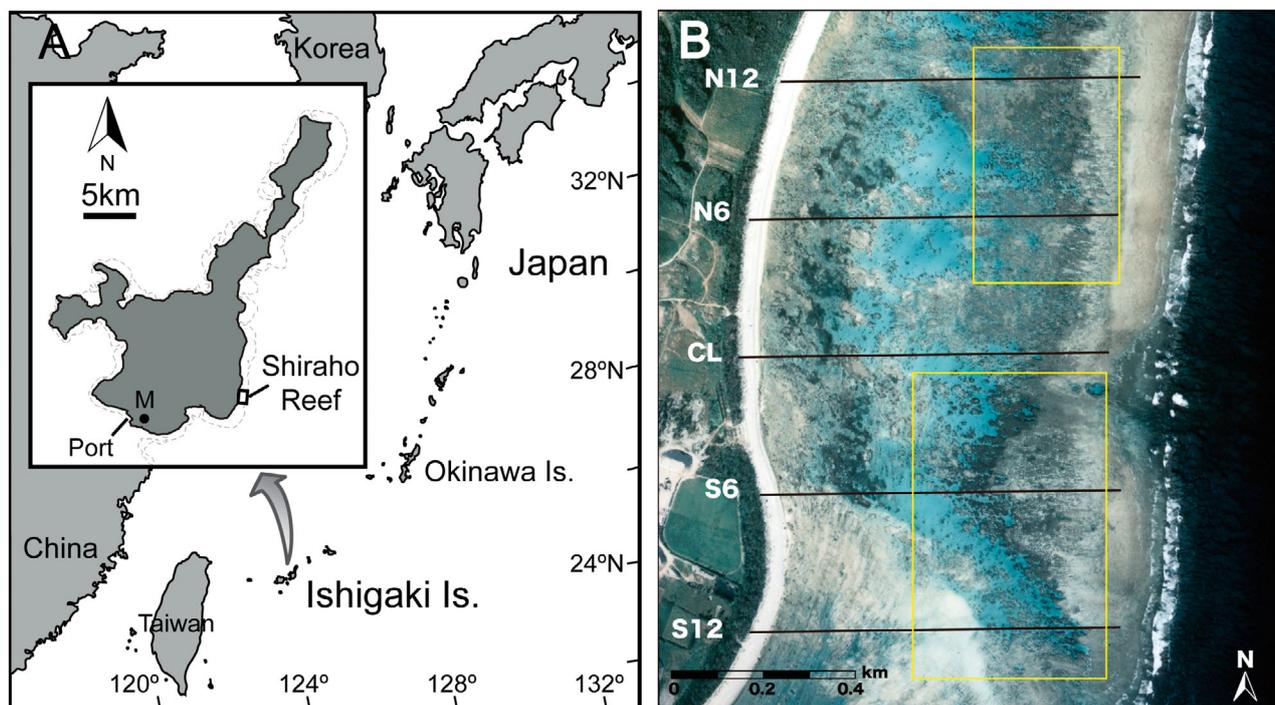
Fig. 1. (A) Location of Ishigaki Island, Ryukyu Islands, southern Japan, and the study site (Shiraho Reef). 'Port' stands for Ishigaki port, where water temperature was measured from 1998 to 2003. Wind speed data were obtained at the Ishigakijima Local Meteorological Observatory (M) (24° 20.2′ N, 124° 9.8′ E). (B) Aerial photograph of Shiraho Reef showing 5 transects (black lines). Shiraho Reef is a well-developed fringing reef with a reef flat of 750 to 800 m width. Yellow squares indicate the areas that were analysed by aerial photographs

were chosen as follows: before bleaching (May 1998), recovery (2003), decline (2008) and present (2012), based on changes in net coral area (see Fig. 2). Year was included as an explanatory variable (categorical factor), and net area was a response variable. The analysis was performed using the statistical software Statistica 06J (StatSoft).

Five aerial photographs were used to determine spatial changes in coral patches between 1995 and 2006 (Table S1 in the Supplement at www.int-res. com/articles/suppl/m509p171_supp.pdf). All photographs were georeferenced and normalised to remove influences from differences in image acquisition conditions using digital number values related to the intensity of solar radiation reflected in sand and deep water by referring to the image taken on 20 September 2006. We performed a supervised classification using a Mahalanobis distance classifier of all aerial photographs based on *in situ* transect survey information (Palandro et al. 2008). The Mahalanobis distance classifier is a direction-sensitive distance classifier that uses statistics for each class, and assumes that all class co-variances are equal (Yuan et al. 2014). We defined 2 classification categories as high coral cover (50–100% cover) and low coral

cover (5–50% cover) on the basis of an earlier map produced by the Ministry of the Environment, Government of Japan (1994). After completion of the area classification, we manually corrected erroneous classifications along the shoreline and reef crest where corals do not exist and recalculated the area of each category. Moreover, 4 coral patches were delimited as polygons by visual assessment, and their area was calculated from the same aerial photographs (Fig. 1B). The patches were selected as *Montipora* (3 patches, between Transects N6 and N12, around N6 and S12) and *Heliopora* (1 patch, around Transect S6) based on field observations in addition to the past records (Kayanne et al. 2002, Harii & Kayanne 2003). Relative changes in patch area were calculated with reference to the area at the beginning (January 1995), which was set equal to 100%.

Seawater temperature data were obtained from the Japan Meteorological Agency (JMA) for the years 1998 to 2003 (measured at the sea surface at Ishigaki port; Fig. 1A) and from the WWF Coral Reef Conservation and Research Centre, Japan, for the years 2003 to 2012 (measured at 2 m depth in the northern part of Shiraho Reef using a temperature logger; HOBO Water Temp v2, ±0.2°C). Water temperature

was measured hourly in Ishigaki port and was recorded every 10 to 20 min at Shiraho Reef. The daily average from both data sources was calculated. The overlap in data between 2003 and 2005 allowed comparisons of the temperature at Ishigaki port and Shiraho Reef. In addition, the Degree Heating Week (DHW, Liu et al. 2003, 2006) around Ishigaki Island was calculated as an indication of long-term trends (1982 to 2011) in thermal stress; the DHW was based on weekly means of sea surface temperatures (SST) obtained by satellite and provided by the US National Oceanic and Atmospheric Administration (NOAA; http://apdrc.soest.hawaii.edu/dods/public_data/NOAA_SST/OISST/). DHW represents the accumulation of the anomalies exceeding the maximum of the monthly mean SST (August in Ishigaki Island) over a rolling 12 wk period (Liu et al. 2003, 2006). Maximum seawater temperatures for each year during the same periods were also determined.

Catastrophic damage to coral reefs by storms occurs when the maximum wind speed exceeds 33 m s^{-1} (Fabricius et al. 2008). Therefore, we examined historic track records for severe typhoons that reached this wind speed threshold between 1996 and 2012 (see www.data.jma.go.jp/fcd/yoho/typhoon/position_table/ (in Japanese); similar data are available in English at Best Track Data www.jma.go.jp/jma/jma-eng/jma-center/rsmc-hp-pub-eg/besttrack.html). Maximum wind speed data were obtained at the Ishigakijima Local Meteorological Observatory of the JMA, 9.7 km from Shiraho Reef (Fig. 1A). Significant wave heights and lengths (the mean wave height and length of the highest third of the waves) of selected typhoons were also obtained from the coastal wave analysis chart at the closest coastal grid

point, 46.4 km from Shiraho Reef (Point O, 24° 30' N, 124° 35' E), as provided by the JMA.

RESULTS

Temporal changes in net coral area

The coral area of all taxa at Shiraho Reef changed dramatically between 1998 and 2012 (Fig. 2). The net area along all transect lines was 170.6 m^2 at the beginning of this study in May 1998. The relative net area changed from 100% in May 1998 to 28 ± 7% (±SE, n = 5) following the mass bleaching in December 1998. The relative net area then increased to 96 ± 7% (170.5 m^2) by 2003, after which it again decreased to 54 ± 9% by August 2008, although a slight increase was noted at the end of the study, in October 2012 (Fig. 2).

The average net coral area along transect lines varied among coral taxa (Fig. 3) but did not change significantly between 1998, 2003, 2008 and 2012 in any taxa except for *Pavona* (GLM 1-way ANOVA: *Montipora*, $F_{3,16}$ = 1.76, p = 0.196; massive *Porites*, $F_{3,16}$ = 0.53, p = 0.667; branching *Porites*, $F_{3,16}$ = 0.128, p = 0.942; *Heliopora*, $F_{3,16}$ = 0.38, p = 0.766). Branching *Montipora* spp., *Acropora* spp. and *Pavona* (only observed at 2 transects) followed similar trends over time, but with greater variation in *Montipora*. These corals were significantly affected by the 1998 coral bleaching event, after which there were mean increases in net area to 2003. However, after 2005 the net areas of both *Montipora* and *Acropora* declined significantly until 2008 and showed very little change thereafter. For example, the maximum coral cover of *Montipora* in May 1998 along Transect N12 (40%, be-
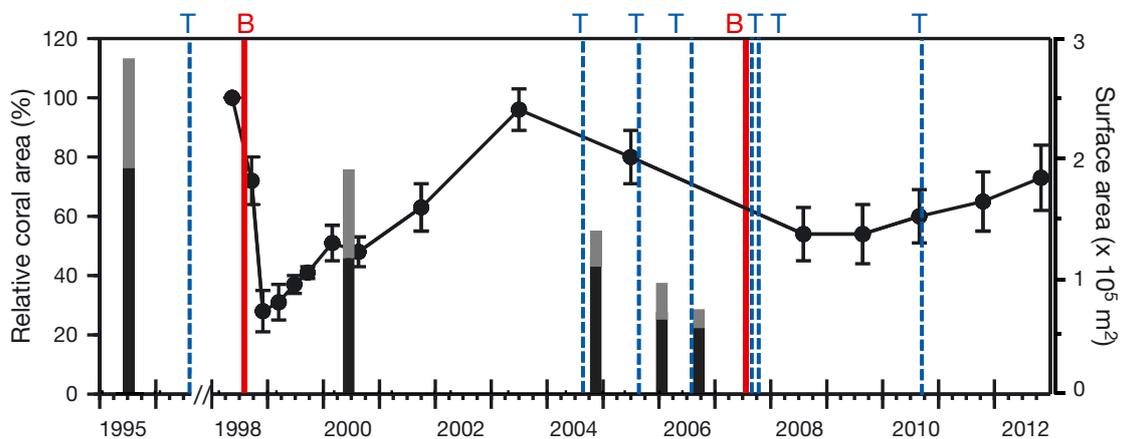

Fig. 2. Temporal relative changes in total net area for 6 coral taxa along 5 transects from 1998 to 2012 and the surface area of coral coverage of 50–100% (black bars) and of 5–50% (grey bars) in aerial photographs taken between 1995 and 2006 at Shiraho Reef. Transect data from 1998 to 2000 were from Kayanne et al. (2002). B: bleaching (red lines); T: typhoons (blue lines)
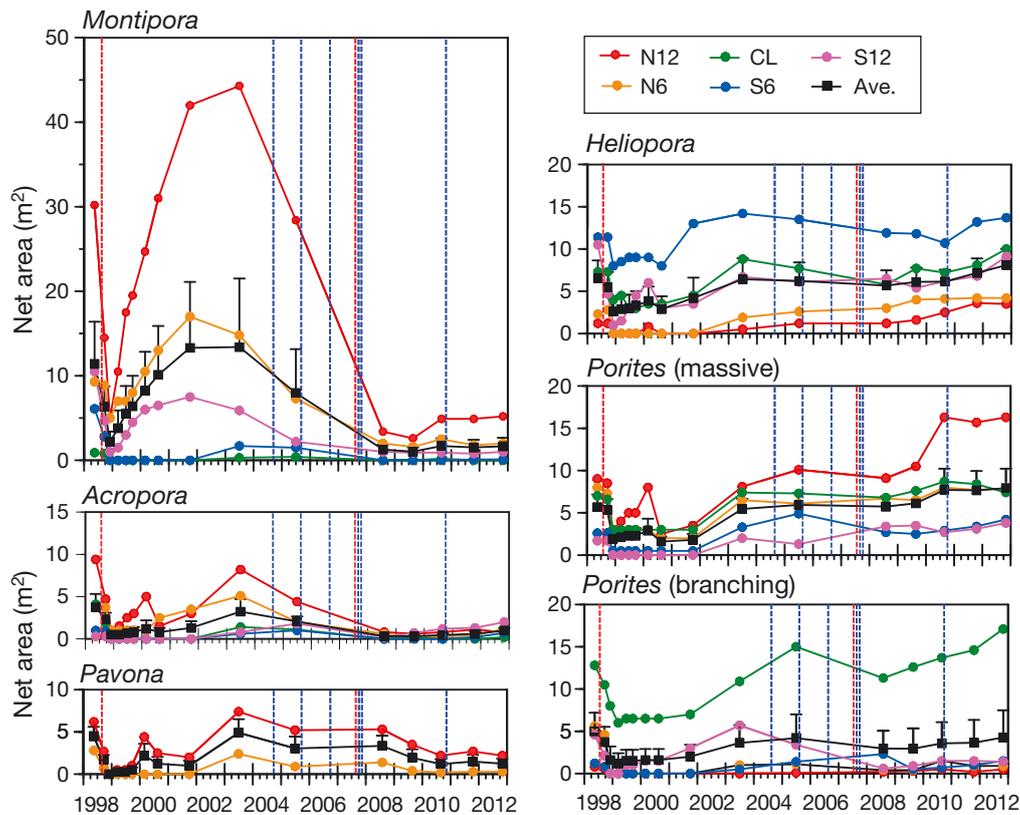
Fig. 3. Temporal changes in the net area of each coral taxon along the 5 transects (represented by different colours) at Shiraho Reef from 1998 to 2012. Ave. indicates the average net area of the 5 transects (+SE). Red and blue dashed lines indicate bleaching and typhoons, respectively

tween 580 and 590 m from the shoreline) dropped to 20% after the bleaching event and then increased to 60% by 2000. After 2005, it drastically decreased to 1% by 2008. In contrast, massive and branching *Porites* spp. and *H. coerulea* were less impacted by the 1998 bleaching event and recovered slowly through 2003. After this time, the net area of these corals did not change or only increased slightly (Fig. 3). For example, massive *Porites* were distributed continually between 70 and 180 m along Transect N12 with 1 to 10% cover, and the cover did not change, or it even increased to 5–10% by 2012. *Heliopora* was dominant from 390 to 530 m of Transect S6 with 5 to 10% cover in May 1998. This coral generally increased up to 15% cover, especially on the shore side (with a maximum at approximately 410 to 420 m) by 2012, although it decreased at one point to 1% on the offshore side (between 460 to 530 m) in 2008.

Spatial and temporal changes in coral communities detected using aerial photographs

The photographic time-series revealed a steady loss in the coral communities from 1995 to 2006 throughout Shiraho Reef (Fig. 2, and see Fig. S1 in the Supplement). The surface area of the communities was $2.8 \times 10^5 \, m^2$ in January 1995 but decreased to $1.9 \times 10^5 \, m^2$ by 2000 and to $0.7 \times 10^5 \, m^2$ by 2006, which was 25% of the initial area (Fig. 2). Three coral patches dominated by *Montipora* were similar in size between 1995 and 2000; however, they decreased in 2004 and 2006 to 20% of the initial size (Fig. S2). In contrast, a large patch of *Heliopora* did not change over time (Fig. S2).

Seawater temperature and typhoon records

Maximum temperatures on the reef flat at Shiraho Reef regularly exceed 30°C in summer (Fig. S3). The DHW exceeded 4°C in 1983, 1988, 1993, 1998, 2001, 2003 and 2007, whereas coral bleaching was observed only in 1998 (DHW 13.3°C) and 2007 (DHW 6.2°C; Fig. S4). The maximum temperatures recorded were 31.2 and 30.7°C from NOAA SST data in 1998 (23 to 29 August) and 2007 (29 July to 4 August), respectively, and these peaks in temperature corresponded with bleaching events. The temperature at Shiraho Reef also reached 32.1°C on 30 July 2007 (Fig. S3).

Shiraho Reef was affected by 7 severe typhoons between 1996 and 2012. The impact of typhoons was especially severe from 2004 through 2007, when the reef was hit every year (Fig. 2, Table S2). The maximum wind speed ranged between 33.6 and 48.2 m s^{-1}, and significant wave heights were reached (between 7.8 and 12.2 m; Table S2). Typhoon 200417 ('Aere') in 2004 caused the loss of corals observed between 2003 and 2005 in the transect data and between 2000 and 2004 in the aerial images. Following this event, severe typhoons passed over or near Shiraho Reef in both 2005 and 2006.

DISCUSSION

Temporal changes in coral area at Shiraho Reef

Coral area at Shiraho Reef decreased after the 1998 bleaching event, due to high thermal stress, but showed a rapid recovery by 2003 (Kayanne et al. 2002, this study). After this recovery, the coral area again decreased between 2004 and 2008 as revealed by both the transect data and the aerial photographic data. Multiple disturbances, including 2 bleaching events and several typhoons, were most likely the cause of the decrease in coral area.

Seawater temperatures were especially high in 2007 (DHW was 6.2°C, with a maximum temperature of 31.2°C), and coral bleaching occurred during this thermal event. This bleaching event was widely observed around Ishigaki Island; for example, 60% of acroporid corals had died because of bleaching by October 2007 in Sekisei Lagoon (Nojima & Okamoto 2008, Dadhich et al. 2012). A high mortality due to bleaching was observed in tabular and corymbose *Acropora* at Iriomote Island, which is located approximately 20 km west of Ishigaki Island (Muko et al. 2013). The bleaching event in 2007 was not as severe as that in 1998 with DHW of 13.3°C, but the recovery was slower after 2007.

Before and after this bleaching event, strong typhoons passed over Shiraho Reef. Five typhoons of varying severity triggered a dramatic decrease in coral area at Shiraho Reef before the bleaching in 2007, with a nearly 50% reduction between 2004 and 2006 (aerial photographic data). In addition, just after the 2007 bleaching, 2 strong typhoons passed in the autumn of the same year. The observed decrease in coral net area can be explained as a result of the splitting of large patches into small coral patches between 2004 and 2007 through storm action. The resulting patches were too small to recover after bleaching in

2007. In contrast, from 1996 until 2004, no severe typhoons struck Shiraho Reef, and after the 1998 bleaching event, corals with large patches exhibited substantial recovery into 2004.

Thermal stresses resulting in bleaching affect smaller coral patches more strongly compared to larger ones (Dadhich et al. 2012). At Shiraho Reef, small patches of branching *Montipora* had already failed to recover after the bleaching events in 1998 and 2000 (Kayanne et al. 2002). Large patches contribute to rapid recovery, likely because they contain larger branches and have more reserves to deal with the stress induced by bleaching until conditions become favourable again. In addition, after bleaching, branching corals are more easily broken by wave action. In a large patch, the broken branches might get entangled with other branches, with this physical stabilization favouring recovery. In a small patch, the broken branches will more easily roll out of the patch and will not be able to stabilize on substrata, which is necessary for their recovery. The recently observed slow recovery was probably influenced not only by thermal stress but also by severe typhoon events.

The present study identifies the frequency of typhoons as a factor that strongly influences the ability of corals to recover from bleaching events and other damage. The physical damage to corals in the Caribbean and the Great Barrier Reef by tropical storms has previously been documented (Knowlton et al. 1981, Hughes 1994, Fabricius et al. 2008), although these storms sometimes reduce bleaching (Manzello et al. 2007) or increase the biodiversity of corals (Connell et al. 1997).

In addition to the physical action of water movement, tropical storms cause heavy rainfall relative to other precipitation systems (Lawrence & Gedzelman 1996). Typhoon rainfall enhances terrestrial discharge from rivers and potentially from groundwater as well, increasing reef nutrient and sediment levels (Blanco et al. 2008). A river located north of Shiraho Reef is a major source of nitrate (Yamazaki et al. 2011), which is likely derived from the agricultural watershed (Umezawa et al. 2002). Because even brief exposure to silt-sized and nutrient-rich sediment can stress corals (Weber et al. 2006), soil runoff after heavy typhoon-associated rains likely contributed to the damage to corals reported here.

The results of the present study, which monitored corals at Shiraho Reef over several years, indicate that coral communities decreased due to the frequency and multiplicity of stresses, including high seawater temperatures, frequent typhoons in closely-

spaced years and nutrient enrichment and sedimentation. Multiple disturbances have also been reported in some other regions. For example, total coral cover declined following a bleaching event and a cyclone in Moorea. However, there was no significant effect of 3 subsequent bleaching events, and coral cover recovered to nearly the same level as before the disturbances; *Montipora* and *Pocillopora* declined, whereas *Acropora* and *Porites* recovered or increased (Adjeroud et al. 2009). For the Great Barrier Reef, nutrient-rich coastal water reduces resistance to coral bleaching more than oligotrophic oceanic water (Wooldridge & Done 2009). Similarly, corals at localities with high chlorophyll *a* (chl *a*) and dissolved inorganic nitrogen (DIN) concentration show higher bleaching prevalence than corals at locations with low chl *a* and DIN (Wagner et al. 2010). Anthropogenically turbid coral reefs are also more vulnerable to bleaching events than less turbid areas in Okinawa Island (Hongo & Yamano 2013). Considering water quality, different recovery patterns may result from lower levels of sedimentation or eutrophication in Moorea compared to Shiraho Reef, where human activities have led to intense development in the adjacent terrestrial area (Hasegawa 2011). Indeed, an isolated coral reef in Western Australia showed less impact from human activities over a decade of observations (Gilmour et al. 2013).

Resilience of corals and community shift

Various disturbances affect coral taxa differently. At Shiraho Reef, branching corals such as *Montipora* and *Acropora* disappeared by 2009, although they had initially recovered after the bleaching event of 1998 (Kayanne et al. 2002). Conversely, *Porites* and *Heliopora coerulea* were less damaged or even increased in abundance throughout the study period.

After bleaching, branching corals generally suffer higher mortality than massive corals (Loya et al. 2001, Baird & Marshall 2002, Pratchett et al. 2011). In addition, they are more readily destroyed by storms than foliaceous, encrusting and massive corals (Woodley et al. 1981). At Shiraho Reef, bleaching and frequent storms fragmented the branching coral community into smaller patches, preventing subsequent recovery. There are 2 possible reasons. First, the failure to recover probably results from a detachment from the substratum and the additional physical damage caused by rolling, as mentioned previously. Similarly, most fragments of branching *Acropora* fail to establish themselves on substrata

after a typhoon (Muko et al. 2013). Second, small fragments may not grow fast enough to stabilize; fragments of the branching coral *A. cervicornis* have relatively low rates of survival and rarely produce new branches (Mercado-Molina et al. 2014). Although branching corals, such as *M. digitata*, on reef flats are known to be asexually distributed by fragmentation (Yamano et al. 2000), a high frequency of bleaching and storms will fragment the community beyond the possibility of recovery. Moreover, soil runoff induced by typhoon rainfall apparently affected branching corals.

Montipora spp. became a 'winner' after the 1998 bleaching event, but was a 'loser' due to bleaching and typhoons at Shiraho Reef over the long term. Our results differ somewhat from observations that show *M. digitata* as a 'loser' over the short term (Loya et al. 2001) but a 'winner' over the long-term via remnant survival and rapid regrowth and that *P. cylindrica* is a 'loser' over the long term at Sesoko Island, Okinawa (van Woesik et al. 2011). This difference might result from the different disturbances at the 2 locations. Two thermal stress events occurred at Sesoko Island, in 1998 and 2001 (van Woesik et al. 2011), whereas at Shiraho Reef, the 2 thermal stresses occurred in 1998 and 2007, along with several typhoons that likely caused physical damage and soil runoff. A 'winner coral', *Goniastrea aspera*, which is known as an environmentally tolerant species, became a 'loser' over the long term after bleaching in a reef flat at Phuket, Thailand, due to size-specific mortality (high mortality was observed in large colonies; Brown et al. 2014). Winners and losers may not be fixed to taxa but may change depending on the disturbances and the sizes of patches or colonies of corals.

Among branching corals, the difference observed in *P. cylindrica*, which recovered and even increased along one transect, could be explained by specificities in the biology of this species. The combination of heat-resistant symbiotic algae and high concentrations of critical host proteins was assumed to provide *P. cylindrica* with better resistance to heat stress (Fitt et al. 2009). Moreover, although classified as 'branching' coral, *P. cylindrica* has a much more resistant skeletal structure compared to branching *Acropora* or *Montipora*.

In contrast, 2 taxa in our study, viz. massive *Porites* and *Heliopora*, appeared to be the most resilient corals in Shiraho Reef. Although both showed successful recovery and resilience, the strategies employed likely differ. Massive *Porites* are normally known as thermally tolerant species and recover after bleaching (Brown et al. 2014). Their mortality is lower

than acroporid corals after bleaching (Baird & Marshall 2002). This resilience is considered to be due to their thicker tissues compared to other taxa (Loya et al. 2001). In addition, massive corals are generally more resistant to turbid conditions than branching corals (Anthony et al. 2007). Moreover, massive corals such as *Porites* and *Montastrea annularis* suffer less physical damage from storms (Woodley et al. 1981, Hongo et al. 2012). Regarding *H. coerulea*, this species is most abundant in equatorial waters where the seawater temperature ranges between 28 and 29°C (Zann & Bolton 1985); it therefore may be more tolerant of thermal stress than other species. These factors could explain why *Porites* and *H. coerulea* showed better survival after multiple disturbances in this region compared to other genera. Similarly, both massive *Porites* and *H. coerulea* significantly increased after bleaching at the Gilbert Islands of Kiribati after a bleaching event in 2004 (Donner et al. 2010). The cover of *Porites* showed small changes 6 yr after bleaching in Western Australia, probably because of its slow regrowth and low reproductive output (Smith et al. 2008). In the present study, the rapid increase in coral cover after bleaching in 1998 can be explained by the rapid recovery of branching *Montipora* spp. and *Acropora* spp. (Kayanne et al. 2002), whereas the recent gradual increase in coral cover was explained by the recovery of other genera.

In the present study, asexual growth and fragmentation played a major role in the recovery process. In addition, new coral recruitment by sexual reproduction also plays an important role in the recovery of corals (Connell et al. 1997, Hughes et al. 2003). Coral juveniles increased in number and contributed to a decade-long recovery following a mass bleaching event in Western Australia (Gilmour et al. 2013). Similarly, coral recruits, especially *Acropora* and *Montipora* spp., likely contributed to reef recovery at northern Okinawa Island after the massive bleaching event of 1998 (Cabaitan et al. 2012). On the other hand, the low cover of *Acropora* spp. (<1% of the benthos) was likely a result of recruitment failure in the southern Arabian Gulf (Burt et al. 2011). Shiraho Reef is a well-developed fringing reef where the reef flat is separated from the outer reef by exposure of the crest during low tide (Kayanne et al. 1995, Harii & Kayanne 2003). At Shiraho Reef, one of the dominant corals, *H. coerulea*, is a brooder that releases planula larvae (Harii et al. 2002); juveniles were observed around adult colonies between 1998 and 2000 (Harii & Kayanne 2003). In the same study, new recruits of the brooder *Pocillopora damicornis* were observed but no recruits were noted for spawners that release egg-sperm bundles (S. Harii pers. obs.). The other dominant corals at the study site are spawners, and it takes several days before the larvae are able to settle (Babcock et al. 1986, Babcock & Heyward 1986). Therefore, different reproductive strategies affect the recovery of corals. The reef structure, with a relatively isolated reef flat, might limit the recruitment of coral planula larvae from other locations, but would present an advantage for the larvae of brooders. Thus, the reef recovery at Shiraho Reef is largely dependent on local recruitment of brooded larvae, asexual growth and surviving fragments rather than on supply and survival of sexual recruits issued from spawning events.

CONCLUSIONS

Our study clearly shows that a shift in the coral taxa from branching *Montipora* and *Acropora* to a *Porites*- and *Heliopora*-dominated reef resulted from multiple disturbances. This combination of factors and the frequency of disturbances explain the differences between our study and other similar recovery studies that have been conducted elsewhere in the world. In the current situation with increased anthropogenic pressure and climate change, water temperature increases are likely to cause additional bleaching events (Frieler et al. 2012) as well as more frequent and stronger tropical storms (Knutson et al. 2010). Those storms will subsequently increase physical damage to coral colonies as well as terrestrial runoff and sedimentation onto the reefs, reducing the survival likelihood of parents and fragments of asexual propagules.

Moreover, the ability of the coral community to recover can vary depending on the mode of sexual reproduction at Shiraho Reef, which is regularly isolated from the outside. If the ocean becomes warmer than at present, patterns of connectivity of spawners would change, due to faster development and high larval mortality (Figueiredo et al. 2014). The study of Figueiredo et al. (2014) indicates that local retention enhances self-recruitment, but leads to less connection between reefs. Once they diminish under the influence of global warming, branching corals such as *Acropora* and *Montipora* at Shiraho Reef are more likely to have difficulty recovering through recruitment, since fewer remnants would produce fewer eggs, and there would be fewer larvae from outside. Therefore, it is essential to increase local management efforts to reduce local reef stressors so that remaining corals can resist and recover from disturbances.

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