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Disappearance and Return of an Outbreak of the Coral-killing Cyanobacteriosponge *Terpios hoshinota* in Southern Japan

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Masashi Yomogida, Masaru Mizuyama, Toshiki Kubomura, and James Davis Reimer (2017) *Terpios hoshinota* is cyanobacteriosponge that can cause serious damage to coral reef ecosystems by undergoing rapid breakouts in which it smothers and encrusts hard substrates, killing living sessile benthic organisms and reducing biodiversity of the affected area. The reasons for these outbreaks are still unclear, as are long-term prognoses of affected reefs. Some reports have suggested outbreaks may not be permanent, but very little long-term monitoring information exists. In this study, we report on a *T. hoshinota* outbreak (~24% coverage) at Yakomo, Okinoerabu-jima Island, Kagoshima, Japan between 2010 to 2014. In this period, the existing outbreak was seen to almost completely disappear (~0%) after unusually severe Typhoon Songda passed by in early June 2011. After this, macroalgae and a cyanobacterial bloom became the dominant benthos, but by September 2014, *T. hoshinota* coverage had recovered to approximately half of its pre-typhoon coverage, suggesting the conditions that had caused the outbreak still persisted at Yakomo. While the conditions promoting *T. hoshinota* growth at this site remain uncertain, it appears that subtropical typhoons could play an important role in the dynamics of *T. hoshinota* outbreaks and disappearances.

Key words: *Terpios hoshinota*, Outbreak, Phase shift, Typhoon, Subtropical coral reefs.

BACKGROUND

Sponges are filtration-feeding organisms, and provide habitat for a variety of marine life including prokaryotes, shrimp, worms, hydroids, zoantharians, and fish (van Soest et al. 2012; Montenegro et al. 2015). In addition, sponges contain symbiotic bacteria, and produce organic matter that contributes to the nitrogen cycle, and thus play an important role in marine ecosystems (van Soest et al. 2012).

On the other hand, there are sponge species that can cause serious damage to marine ecosystems. The sponge species *Terpios hoshinota* Rützler and Muzik, 1993 (phylum Porifera, class Demospongiae, order Suberitida, family Suberitidae) is one such species. This species is in symbiosis with numerous cyanobacteria and is a photoautotrophic organism (Hirose and Murakami 2011; Liao et al. 2011). Distributed in the coral reefs of the Indo-Pacific, it often grows over other benthos, and has been known to undergo outbreaks in shallow coral reefs, causing death to hard corals and other benthos (Rützler and Muzik 1993; Reimer et al. 2011b). By growing approximately 1-2 mm a day (Liao et al. 2011), *T.*

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hoshinota has been reported to overgrow and kill numerous hard coral including genera *Lobophylia*, *Montipora*, *Acropora*, *Merulina*, and *Goniastrea*, resulting in the death of wide areas of coral reefs (Rützler and Muzik 1993).

Terpios hoshinota was first discovered in Guam (Bryan 1973), and later reported from the Northern Mariana Islands, Western Caroline Islands, the Philippines, and American Samoa (Plucer-Rosaria 1987). In more recent years, the species has been reported from southern Taiwan (Liao et al. 2007), Australia's Great Barrier Reef (Fujii et al. 2011), Sulawesi and Java (de Voogd et al. 2013), and most recently it has been recorded in the Indian Ocean, in the Maldives (Montano et al. 2015) and Mauritius (Elliott et al. 2016).

Terpios hoshinota has also been confirmed from the Ryukyu Islands in southern Japan. In 1985-1986 there was an outbreak on the reefs of Tokunoshima Island, Kagoshima, in which many coral colonies were killed, particularly at Yonama coast (Rützler and Muzik 1993), where the species covered up to 87.9% of substrate (Marine Park Center Foundation 1986). From the thin, black, 'coating' this species makes over other benthos, it was reported as the "Black Death" in local media at that time. In subsequent investigations, another outbreak was confirmed at Yakomo site on Okinoerabu-jima Island, Kagoshima, in 2010 (Reimer et al. 2011a).

However, these outbreaks may not necessarily be stable. In a re-investigation of the Yonama, Tokunoshima Island site approximately 25 years after the initial *T. hoshinota* outbreak, results showed that the species had disappeared (= 0%), and the dominant benthos had become *Acropora* hard coral colonies (Reimer et al. 2011a). These results suggest *T. hoshinota* outbreaks are not necessarily 'dead-ends' and coral reefs may recover from outbreaks. However, much remains to be understood regarding the ecology of *T. hoshinota* and the mechanisms of outbreaks.

In this study, in order to understand the progression of outbreaks, we conducted field surveys between 2010 and 2014 to follow changes in *T. hoshinota* coverage at an outbreak site, Yakomo, on Okinoerabu-jima Island in the Ryukyu Islands. Over the same period we also recorded changes in other benthic categories. We then compared the results of this study to previous research and briefly discuss possible factors that may lead to increases or decreases in *T. hoshinota* cover.

MATERIALS AND METHODS

Study area

From March 2010 to September 2014, transect surveys were performed at Yakomo (27°20'N, 128°32'E), China Town, on Okinoerabu-jima Island, Kagoshima Prefecture, Japan, in the Ryukyu Islands (Fig. 1).

On subtropical Okinoerabu-jima Island, the average sea surface temperature is 23°C (China Town homepage: www.town.china.lg.jp/modules/kikakushinkou/index.php?content_id = 166). Yakomo, located on the southwest coast of Okinoerabu-jima Island, has a white sandy beach approximately 3 km in length. A coral reef runs parallel to the sandy beach, with a moat of approximately 180 m width from crest to shore. Between the sandy beach and reef margin, the moat has a depth of up to 5 m (at high tide). The moat terrain generally consists of scattered macroalgae on sand with a few stony corals. In some areas there is carbonate substrate extending for tens to hundreds of square meters.

Terpios hoshinota identification

In this study, we surveyed the same location within Yakomo as previously reported (Reimer et al. 2011b). This previous report also identified the black encrusting cyanobacteriosponge at this site as *T. hoshinota* based on both the external form and internal spicules, with further confirmation of species identity via molecular analyses. In the field, *Terpios hoshinota* can be identified easily as it forms a < 1 mm thin coating that is slightly thicker at areas sheltered from waves and current. The color is bright gray in areas that are exposed to sunlight, and generally darker gray, black, or dark brown in shaded areas. There are osculae (2~3 mm in diameter) visible on the body with peripheral radially arranged astrorhizae (see Fig. 1 in Reimer et al. 2011b).

Transect surveys

Survey of *Terpios hoshinota*

We utilized the line-intercept transect (LIT) method to investigate benthos. Surveys were carried out ten times (March, August, September, October, December in 2010; June, October in 2011; February and May in 2012; and September 2014). Transects were 10 m length and 1 m in width (Beenaerts and Berghe 2005). Five transects were conducted for each survey, except for in September 2014 when ten transects were conducted. The surveys from August 2010 to May 2012 were permanent transects (marked with pegs nailed into the carbonate substrate), with four placed to perpendicular to shore, and one parallel, and all at 2-3 m depths. However, initial transects from March 2010 were not permanent but placed within the Yakomo survey area, while in September 2014 the pegs marking transects had been lost, likely from typhoons, and again we performed non-permanent transects within the survey area (Fig. 1).

All transects (permanent and non-permanent) were separated by 10 to 30 m intervals from neighboring transects on the reef, within an area of approximately 150 × 100 m (Fig. 1). Digital camera images for each transect were taken. Each transect consisted of 25-40 images. We used Adobe Illustrator CS4 to create a continuous connected transect image for each transect that was utilized in subsequent analyses.

Benthic survey image analyses

Benthos captured in survey images were divided into the following categories:

1) *T. hoshinota*, forming a thin coating on coral or hard sediment, black or light gray in color;

2) Macroalgae, including both red and green algae, not including *Ceratodictyon spongiosum* (see #3 below);

3) Sponge algae (*C. spongiosum*), easily distinguishable in the field by dark green or black branching form;

4) Cyanobacteria, visible brown mat-like colonies on the seafloor;

5) Hermatypic corals, including scleractinians and the hydrozoan genus *Millepora*;

6) Dead coral, completely white or bleached

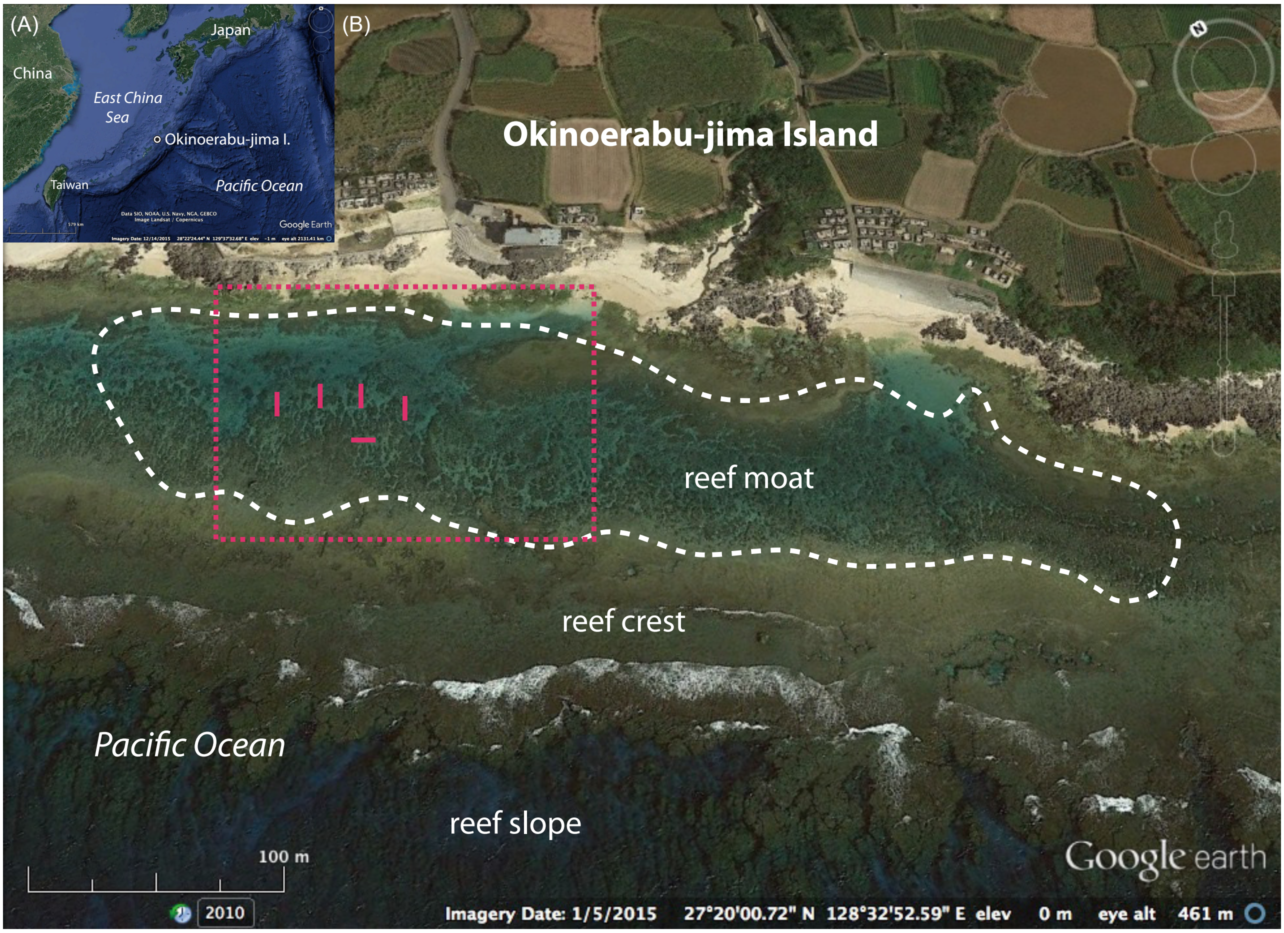

Fig. 1. (A) Location of Okinaerabu-jima Island, Kagoshima, Japan in the northwestern Pacific and, (B) map of Yakomo coast on Okinoerabu-jima Island. Red dotted box shows the *Terpios hoshinota* survey area, white dotted lines show the approximate area of *T. hoshinota* along the coast, and red solid lines approximate locations of permanent transects. Images from Google Earth.

coral, may be covered in algae;

7) Other benthos, including giant clams, zoantharians, soft corals, and all other organisms not covered by categories 1 to 6 above, including mobile sea cucumbers and sea urchins;

8) Sand/carbonate, generally sand, unconsolidated small rubble, or hard carbonate;

9) Unknown, portions of images hard to see due to shading or lack of focus.

The above benthic categories were measured to the nearest mm. Values of each benthic category were then displayed as a percentage the total length (1000 cm). In cases when length of categories could not be confirmed due to twisting of the tape measure or shading, we used ImageJ (National Institutes of Health, USA) to obtain measurements.

Extent of *T. hoshinota* outbreak

To determine the extent of *T. hoshinota* on the Yakomo coast, we conducted a simple snorkel survey in September 2014. Teams of snorkelers swam in both directions (roughly southeast and northwest; Fig. 1) along the coast from the entry point at the survey area at Yakomo. The survey stopped when no *T. hoshinota* was noticed for 100 m since the previous last sighting of *T. hoshinota*. GPS coordinates were taken at the west and east ends of the *T. hoshinota* outbreak, and we then prepared a simple map based on coordinates.

Typhoons

Typhoon data (windspeed, wave height) were obtained from the Japan Meteorological Agency homepage (http://www.jma.go.jp/jma/index.html). As there was no locally available wave data for Okinoerabu-jima Island, we utilized data from the closest available point off Naha, Okinawa-jima Island, Okinawa Prefecture (26°12'44.4"N, 127°40'44.8"E; Ministry of Land, Infrastructure and Transport Port Authority, National Harbor Ocean Wave Information Network (Naufasu)).

Statistical analyses

The percentage data of transects were analyzed in R version 3.3.2 (R Core Team 2016) with the Bray-Curtis similarity index calculated using the percentage data. Subsequently, we also performed a cluster analysis using the Bray-Curtis similarity index. Non-parametric multi-dimensional scaling (NMDS) was utilized for examining the similarity of each survey's data utilizing all nine benthic categories.

RESULTS

Transect surveys

The results of the LIT surveys from March 2010 until September 2014 (*n* = 55 transects) are shown in figure 2 and table S1. Sand and carbonate was the dominant category (Fig. 2), accounting from 50.2% to 89.4% of the total benthic coverage in surveys. Among biological categories, *Terpios hoshinota* was the dominant category from March 2010 to December 2010, and again in September 2014. Macroalgae was dominant in June 2011 and May 2012, while cyanobacteria mats were dominant in February 2012 (Fig. 2).

From March 2010 until October 2010, *T. hoshinota* cover was observed to be 24% or higher (Fig. 2). In December 2010, coverage dropped to 17.6 ± 7.0%, and it then decreased again to 0.02 ± 0.04% in June 2011. Between June 2011 and May 2012, *T. hoshinota* coverage was very low, between 0.02 to 0.3%. However, *T. hoshinota* did not disappear completely, with a few patches of diameters of 5 to 15 cm still present. By September 2014, the coverage had recovered to 11.4 ± 6.8%.

Macroalgae also showed some differences between surveys. Coverage in May 2012 was the highest observed (13.6 ± 6.6%), and was less than 10% in all other surveys (Fig. 2). The large majority of macroalage (~98%) was *Actinotrichia* sp. and the remaining 2% was grass-like seaweed (turf algae).

Cyanobacteria mat coverage was 0% in nine of ten surveys, with the only exception in October 2011, when this was the dominant biological benthic category, covering 39.9 ± 7.5% (Fig. 2).

NMDS and similarity analyses both showed three major groupings: 1) March 2010 to December 2010 plus September 2014 (when *Terpios* was the dominant biological benthos); 2) June 2011 + February 2012 + May 2012, when *Terpios* was absent; and October 2011, when cyanobacteria was the dominant biological benthos (Fig. 3).

No large differences were seen between surveys for sponge algae, hard corals, dead coral, other benthos, or unknown categories, and these values were generally very low, and most often not above 5% in any given survey (Fig. 2). Hard corals were exclusively encrusting morphologies, with no

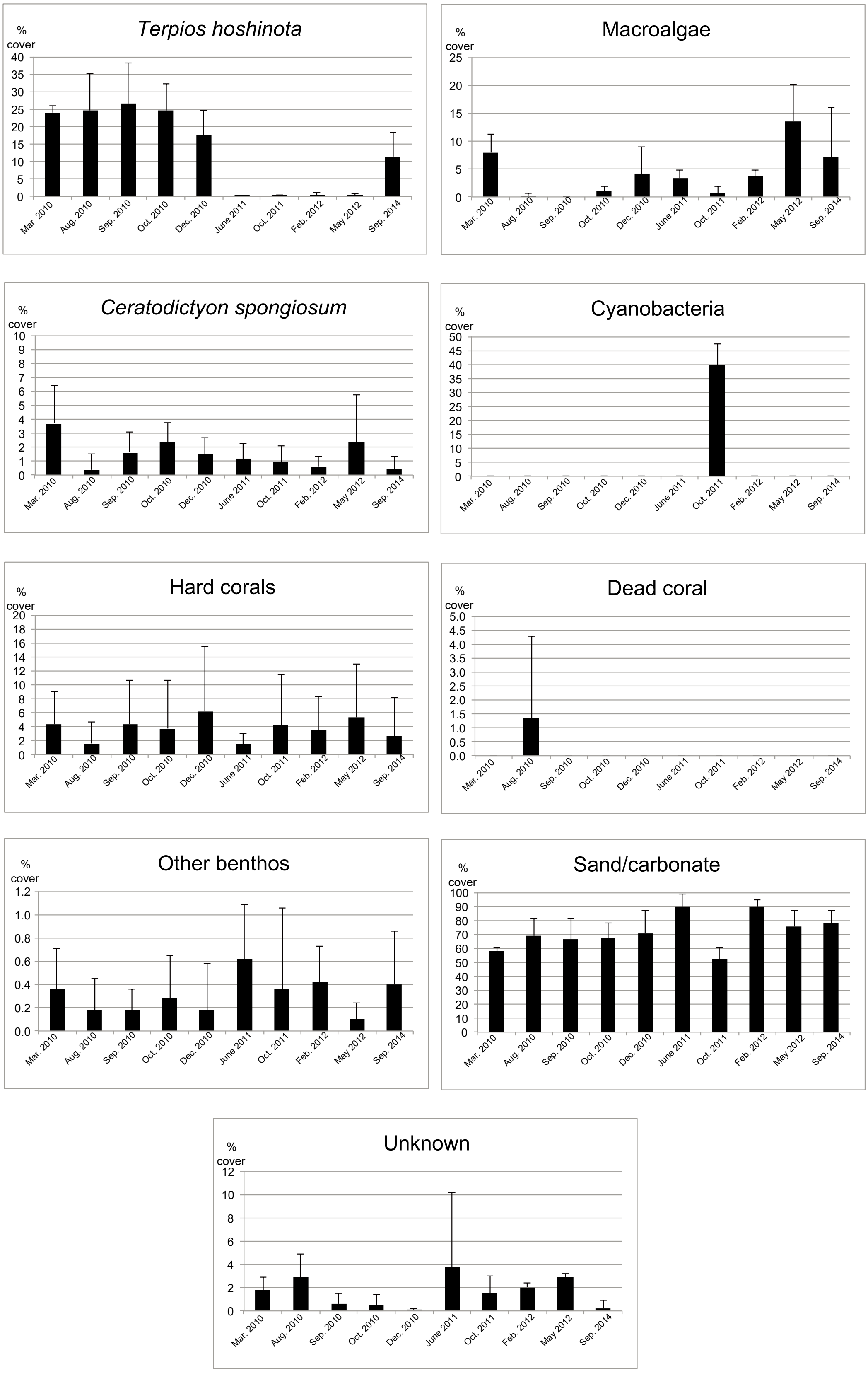

Fig. 2. Coverage of different benthic categories at Yakomo from March 2010 to September 2014. Note the large time gap between the surveys in May 2012 and Sept 2014.

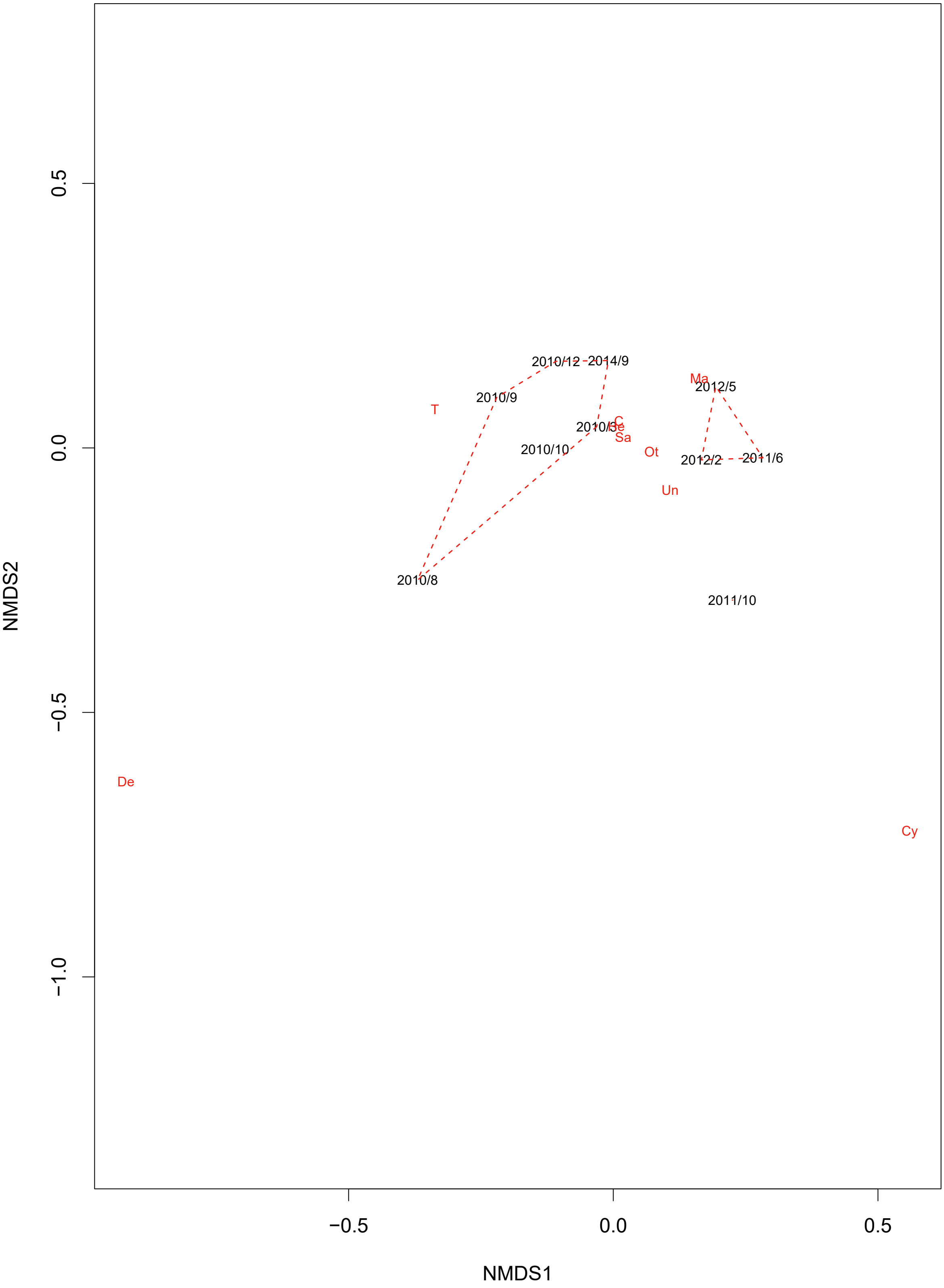

Fig. 3. Non-parametric multidimensional scaling analyses of nine categories of transect data showing three major groupings of survey data (red dotted lines = 75% Bray-Curtis similarity; red letters = relative effect of each benthic category, with abbreviations T = *Terpios hoshinota*, C = *Ceratodictyon spongiosum*, Sa = sand/carbonate, He = hermatypic corals, Ot = other, Un = unknown, Ma = macroalgae, De = dead coral, Cy = cyanobacteria).

branching species observed.

Extent of *Terpios hoshinota* outbreak

By snorkeling, the limits of the occurrence range of *T. hoshinota* were determined to be 27°20'8"N, 128°32'43"E and 27°19'55.3"N, 128°33'01.2"E (Fig. 1). The distance between the east and west edges of the outbreak was approximately 620 m, roughly centered on the area where our monitoring was performed. From the monitoring area, the frequency of *T. hoshinota* gradually reduced towards the east and west edges (data not shown).

DISCUSSION

The non-parametric multidimensional scaling results showed three clear groupings both with non-biological benthic categories included in the analyses (Fig. 3, Table S1) and without the inclusion of these categories (*e.g.* biological data only; data not shown). For the Yakomo site during our survey period, there was clearly dominant benthos for nine out of 10 surveys (*Terpios* or cyanobacteria), and the dominant benthos therefore obviously strongly shaped the community. In other words, the benthic community at Yakomo was clearly different after *Terpios* disappeared between June 2011 and September 2014, but then returned to a relatively similar community with the reappearance of *T. hoshinota* in September 2014. Understanding the causes of the reduction in *T. hoshinota* and the subsequent increase are therefore key to understanding the benthic community at Yakomo.

Causes of decreases in *T. hoshinota*

There was an obvious reduction of *T. hoshinota* some time during the period between December 6, 2010 and June 17, 2011. There are two factors that possibly caused the reduction of *T. hoshinota*, both related to typhoons.

In the vicinity of Okinoerabu-jima Island, maximum wave height of Typhoon Songda was 10.22 m on May 28, 2011. When category 3 or 4 Typhoon Songda was positioned at 27°4'N, 128°0'E (near Okinoerabu-jima Island), the maximum wind speed of 38.58 m/s (139 km/h). The waves and wind caused by Typhoon Songda might have peeled off *T. hoshinota* colonies from the substrate. Waves approaching 5 or 6 m are experienced every year in the Ryukyu Islands, both in summer from typhoons and in winter from storms, but wave heights of >8 m were only seen this one time during the survey period, suggesting that these waves were abnormally large for the region.

It is also possible that the decrease was due to sand deposition from Typhoon Songda. In the transect photographs of June 2011 after Typhoon Songda *T. hoshinota* appears white compared to as in images from other dates, and we observed sand deposited upon sponges and algae in the June 2011 survey. Although there was a time lapse of 19 days between Typhoon Songda and our survey on June 17, 2011, our observations show that the influences of this typhoon may have remained at this time. Regardless of whether the cause of *T. hoshinota* decreases was from wave damage or sand deposition, Typhoon Songda is the strongest candidate for observed decreases. Similar results have been suggested in a previous study at Green Island and Lanyu Island (Orchid Island) in Taiwan, where the main cause of reduction of *T. hoshinota* in 2009 was suggested to be Typhoon 8 (Morakot) (Chen 2011).

Between 2013 until the last survey date on September 21, 2014, four additional large typhoons approached Okinoerabu-jima Island, however *T. hoshinota* cover had increased by the September 2014 survey. None of the typhoons approached wave size as seen in Typhoon Songda (all typhoons with wave sizes <8 m). Wind and wave strength may play a role in whether or not *T. hoshinota* cover decreases during typhoons, combined with the length of exposure to these typhoon conditions. In order to more conclusively demonstrate the influence of typhoons on *T. hoshinota* coverage there is a need to examine coverage more immediately before and after a direct hit by a very strong typhoon with >8 m waves.

In summary, it appears that the close approach and large waves of Typhoon Songda in June 2011 caused the almost complete reduction of *Terpios* at Yakomo, although the exact mechanism (waves, burial by sand) remains to be elucidated.

Causes of outbreak and re-appearance of *T. hoshinota*

Terpios hoshinota has a high density of endosymbiotic cyanobacteria (Hirose and Murakami 2011), and in some cyanobacterial sponge species the internal interface between the host and cyanobacteria has been shown to provide both nitrogen-fixing products and photosynthetic products (Cheshire et al. 1997). Around Pagan Island in the Mariana Islands, volcanic ash due to Pagan Volcano activity was deposited on coral reefs in 2009-2010, and at the same time there was a sudden outbreak of cyanobacteria and the appearance of a large patch of *T. hoshinota* (Schils 2012). Subsequently, along with a cessation of the volcanic activity in 2011, outbreaks of cyanobacteria also ceased. When volcanic ash is dissolved in seawater, trace metals that affect organisms such as iron are immediately made available to primary producers (Frogner et al. 2001). From this, Schils (2012) hypothesized that on the coral reefs of Pagan Island an increase in iron concentration may have caused cyanobacteria and *T. hoshinota* outbreaks. In addition, Schils (2012) suggested that outbreaks may occur from not only the chemical components of volcanic ash, but also from sedimentation, via human origin such as shipwrecks, by sediments associated with natural phenomena such as forest fires and wildfires in flue dust, or via desert sandstorms. Similarly, it has been proposed that increased concentrations of iron, phosphates, and nitrites may be responsible for cyanobacterial blooms (Ng et al. 2012). Future research focusing on potential causes listed in Schils (2012) may help clarify environmental mechanism(s) behind *Terpios* outbreaks.

Another possible reason *Terpios* outbreaks were not observed at any location asides from the Yakomo coast may be due to the low dispersion ability of *T. hoshinota*. Many sponge species occur in localized regions due to the poor swimming ability of larvae and/or a predominance of asexual reproduction (van Soest et al. 2012). *Terpios hoshinota* is no exception, as larvae have negative buoyancy, and it has been observed in tank experiments that cyanobacteria-containing larvae settle at very close distances to parents on dead coral substrates, suggesting the species has short larval dispersion distances in the field (Wang et al. 2012; Hsu et al. 2013; Nozawa et al. 2016). Therefore, even if environmental conditions susceptible to outbreaks in other regions are present, *T. hoshinota* may not be able to effectively disperse (Nozawa et al. 2016). However, typhoons may increase long-range dispersal of this species (Nozawa et al. 2016), and the subtropical Ryukyu Islands have the highest incidence of typhoons in the world. Furthermore, *T. hoshinota* can extend thin tissue threads to spread locally across unsuitable habitats (Soong et al. 2009). Given this and the fact that *T. hoshinota* is widespread in the central and southern Ryukyu Islands (Reimer et al. 2011b), we do not consider dispersal limitations to be a significant factor in causing the outbreak to be locally limited to Yakomo on Okinoerabu-jima Island.

In summary, both the original cause of the *T. hoshinota* outbreak at Yakomo and the cause(s) of its partial recovery by September 2014 remain unclear, although it is likely due to a combination of local recruitment, fast growth rates (approximately 1-2 mm per day; Liao et al. 2011), and underlying environmental factor(s).

CONCLUSIONS

From previous research in Taiwan (Chen 2011) and this study, it appears that in subtropical regions typhoons may play an important role in the dynamics of *T. hoshinota* outbreaks. Other previous work from Tokunoshima Island in Kagoshima has shown that outbreaks may not necessarily be a ‘dead-end’ phase shift (Reimer et al. 2011b), and it can be concluded that subtropical *T. hoshinota* outbreaks have the potential to change rapidly.

It has been theorized that *T. hoshinota* is expanding its range in the Indo-Pacific (van der Ent et al. 2016), including into tropical regions such as Indonesia (Madduppa et al. 2017) and the Maldives (Montano et al. 2015). Tropical regions generally do not experience typhoon events, and thus care should be taken to not extrapolate monitoring results from tropical regions to the subtropics: it may be that the dynamics of *T. hoshinota* are very different in the absence of large storm events. For example, outbreaks in Indonesia have been reported to persist for at least four years (Madduppa et al. 2017). Comparisons of long-term monitoring data between tropical and subtropical *T. hoshinota* outbreaks are clearly needed to examine this potential issue.

Additionally, transect surveys at various sites should be carried out more regularly to confirm the trends of increases or decreases of *T. hoshinota* with more accuracy. Moreover, in order to identify the cause(s) of changes in coverage, it is necessary to further examine temporal changes of coastal environmental conditions (typhoons, water quality, seawater temperature, etc.).

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Table S1. Bray-Curtis Dissimilarity Index between each survey. (download)