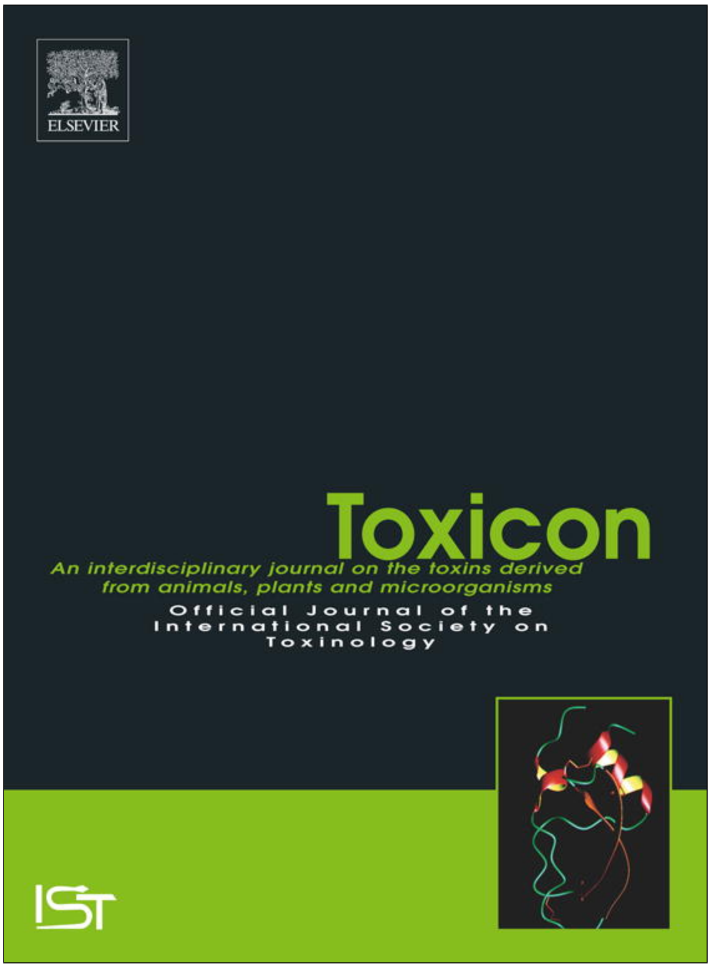

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The effects of natural disturbances, reef state, and herbivorous fish densities on ciguatera poisoning in Rarotonga, southern Cook Islands

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A B S T R A C T

Ciguatera poisoning is a critical public-health issue among Pacific island nations. Accurately predicting ciguatera outbreaks has become a priority, particularly in Rarotonga in the southern Cook Islands, which has reported the highest incidence of ciguatera poisoning globally. Since 2006, however, cases of ciguatera poisoning have declined, and in 2011 ciguatera cases were the lowest in nearly 20 years. Here we examined the relationships between cases of ciguatera poisoning, from 1994 to 2011, and: (i) coral cover, used as a proxy of reef state, (ii) the densities of herbivorous fishes, and (iii) reef disturbances. We found that coral cover was not a good predictor of cases of ciguatera poisoning, but high densities of the herbivorous fish *Ctenochaetus striatus* and reef disturbances were both strong predictors of ciguatera poisoning. Yet these two predictors were correlated, because the densities of *C. striatus* increased only after major cyclones had disturbed the reefs. Since 2006, the number of cyclones has decreased considerably in Rarotonga, because of the climatic shift toward the negative phase of the Pacific Decadal Oscillation. We suggest that fewer cyclones have led to decreases in both the densities of *C. striatus* and of the number of reported cases of ciguatera poisoning in Rarotonga.

1. Introduction

Coral reefs around the world are experiencing shifts toward less desirable states because of a range of disturbances, including eutrophication (Bell, 1992; Lapointe, 1997), *Acanthaster planci* infestations (Done, 1987), disease (Lessios et al., 1984; Hughes, 1994), overfishing (Jackson et al., 2001; Pandolfi et al., 2003; Bellwood et al., 2004), run-off from poor land-use practices (van Woesik et al., 1999), and global climate change (Glynn, 1984; Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Veron et al., 2009). Outbreaks of ciguatera poisoning, which is the most common form of seafood intoxication globally (Baden et al., 1995), have been also linked to reef disturbances (Bagnis, 1994).

The influence of disturbances on outbreaks of ciguatera poisoning is here defined as the new-surface hypothesis. This hypothesis suggests that reef disturbances provide space for opportunistic macroalgae, the preferred substrate for ciguatoxic dinoflagellates, (e.g. *Gambierdiscus* spp.) that are inadvertently transferred into the food web via grazing of herbivorous fishes or invertebrates (Randall, 1958; Lewis et al., 1994; Bagnis et al., 1980). Several studies have linked disturbances to increased cases of ciguatera poisoning, including, for example, reef damage from boat channel construction (Tebano, 1984), boat anchorage and wrecks (Cooper, 1964), cyclones (Randall, 1958; Banner, 1976; Rongo and van Woesik, 2011), *A. planci* outbreaks (Bagnis et al., 1988), and coral bleaching events (Kohler and Kohler, 1992; Bagnis et al., 1992). Yet some reef

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disturbances occur without any increased risk of ciguatera poisoning. For example, the risk of ciguatera poisoning did not increase after the blasting of a channel in Tuvalu (Kaly and Jones, 1994) or after an outbreak of *A. planci* in the 1970s in Rarotonga, Cook Islands (Rongo and van Woesik, 2011).

Outbreaks of ciguatera poisoning also depend on the presence and density of vectors that transfer the ciguatoxins through the food web (e.g., Randall, 1958; Bagnis et al., 1988; Lewis et al., 1994; Bruslé, 1997). These vectors are most often herbivores, and the influence of herbivory on outbreaks of ciguatera poisoning is here defined as the herbivorous fish-density hypothesis. Bagnis et al. (1988) suggested that a rapid increase in the density of herbivorous reef fishes may play a key role in determining outbreaks of ciguatera poisoning in the Gambier Islands of French Polynesia. The herbivorous fish-density hypothesis has unexpectedly received no further attention since it was first suggested over two decades ago. This study explicitly tests both the new-surface and the herbivorous fish-density hypotheses in Rarotonga, in the southern Cook Islands (Fig. 1). We examine how changes in reef state (i.e., percentage hard coral and algal cover) and herbivorous fish densities influenced the dynamics of ciguatera poisoning over an 18-year period, from 1994 to 2011.

2. Materials and methods

The earliest surveys of the coral reefs of Rarotonga were conducted in 1994 (Miller et al., 1994). Miller et al. (1994) surveyed six sites at three fore reef locations, with two sites at each location (see Fig. 1). Miller et al. (1994) used the line-intercept transect (LIT) technique to assess the reef benthos and the Underwater Visual Census (UVC) technique to quantify fish densities. In 1999, Ponia et al. (1999) surveyed six sites and used the video-transect technique to assess the reef benthos, and the UVC technique to estimate fish densities. In 2003, Lyon (2003) surveyed the

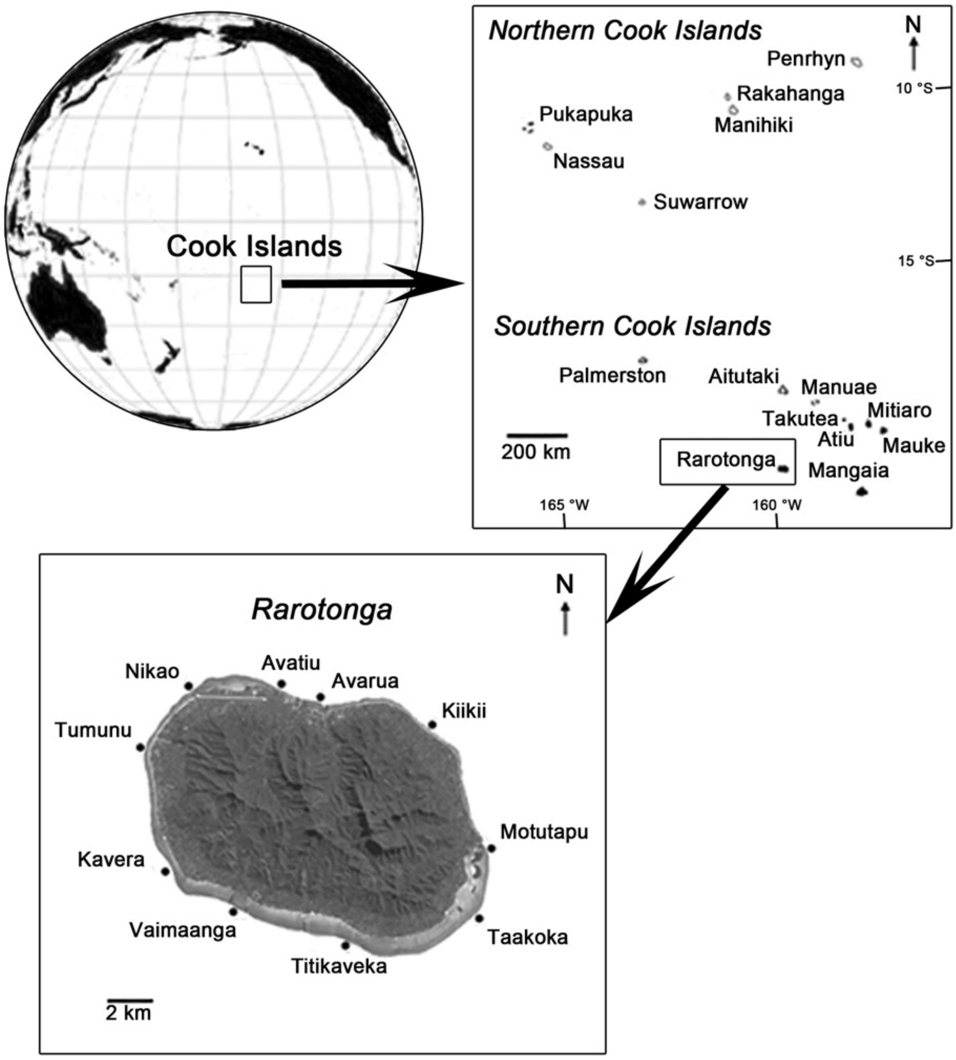

Fig. 1. Location of the Cook Islands delineated in the boxed region. *Top right*: Northern and Southern Cook Islands. *Bottom left*: Rarotonga (21° 12′ S, 159° 43′ W; modified from Google Earth image) depicting the fore-reef sites surveyed in 1994 (Miller et al., 1994, i.e., Avatiu, Motutapu, Titikaveka), 1999 (Ponia et al., 1999, i.e., Avarua, Motutapu, Titikaveka, Kavera, Tumunu, Nikao), 2003 (Lyon, 2003, i.e., Avatiu, Avarua, Kiikii, Motutapu, Taakoka, Titikaveka, Vaimaanga, Kavera, Tumunu, Nikao), 2006 (Rongo et al., 2006, i.e., Avatiu, Avarua, Kiikii, Motutapu, Taakoka, Titikaveka, Vaimaanga, Kavera), 2009 (Rongo et al., 2009a, i.e., Avatiu, Avarua, Kiikii, Taakoka, Vaimaanga, Kavera, Tumunu, Nikao), and 2011 (i.e., Avatiu, Avarua, Kiikii, Motutapu, Taakoka, Titikaveka, Tumunu, Nikao); not all sites were surveyed in each survey year.

benthos using the LIT technique at 10 sites in Rarotonga, but did not survey fish densities.

In 2006, 2009, and 2011 we revisited the general study areas in Rarotonga where previous surveys were conducted. At each site, four haphazardly placed 50-m transects, separated by 10-m intervals, were temporarily set between the depths of 7–9 m. Along each transect, we used the point-quadrat method to record the benthos, using a 1-m^2 quadrat frame that was tossed haphazardly every 5 m along the 50-m transect, for a total of 10 quadrats per transect (40 quadrats per site). The quadrat used to record the benthos was partitioned into 25 sections with string, providing 16 points of intersection. The reef benthos under each intercept was recorded. The benthic survey focused on measuring the percentage cover of hard coral, turf algae ($\leq$1 cm in height) and macroalgae ($>$1 cm in height) (see Steneck, 1988); turf and macroalgae have been reported to host high densities of ciguatoxic dinoflagellates (see Cruz-Rivera and Villareal, 2006). Fish surveys were conducted using the UVC technique, to determine the density of known ciguatoxic herbivorous reef fishes (i.e., acanthurids and scarids; see Rongo and van Woesik, 2011) using replicated 50-m by 4-m wide belt transects.

Information on reef disturbance events (i.e., coral bleaching, *A. planci* outbreaks, and cyclones) was obtained from the literature and from anecdotal reports dating back to 1970 (Table 1). Only disturbance events from 1994 to 2011 were used in the data analysis, because reliable recording of hospital cases of ciguatera poisoning in Rarotonga only commenced in 1994. For each year, disturbance events were placed into one of five categories depending on their severity (with 5 being the most severe). Severity was based on damaging wind speeds (see de Scally et al., 2006; Baldi et al., 2009), and on reef damage observed in Rarotonga (see Goreau and Hayes, 1995; Lyon, 2003; Rongo et al., 2006, 2009a; Rongo and van Woesik, 2011). Hospital records of ciguatera poisoning, from 1994 to 2011, were obtained from the Cook Islands Ministry of Health in 2011 (see Rongo and van Woesik, 2011; for justification in the use of hospital cases).

2.1. Data analysis

A non-parametric Friedman test was used to examine differences in the percentage cover of hard coral, turf and macroalgae, and herbivorous reef-fish densities among years (2006, 2009, and 2011). Sites within years were used as replicates by averaging across transects at each site. Information on macroalgae was not available for years prior to 2006. Herbivorous reef fishes were grouped into three categories prior to analysis. The first category included only one acanthurid species *Ctenochaetus striatus*, a common detritivore (Choat et al., 2004; but see Marshell and Mumby, 2012) considered 'high-risk' for ciguatera poisoning in Rarotonga (Rongo and van Woesik, 2011), and a primary vector of ciguatoxin (Randall, 1958; Yasumoto et al., 1971; Banner, 1984; Lewis et al., 1994; Lewis, 2006). The second category included other acanthurid species, considered 'low risk' for ciguatera poisoning in Rarotonga (e.g., *Acanthurus triostegus*, *Acanthurus guttatus*, *Naso unicornis*, and *Naso lituratus*) (Rongo and van Woesik, 2011), but also included *Acanthurus nigrofuscus*, a common herbivore on Rarotonga's reefs. The third category included parrotfishes (scarids), which are primarily grazers and are 'high-risk' species for ciguatera poisoning in Rarotonga (Rongo and van Woesik, 2011). Plots were generated using *Statistica 6*®, and all comparative analyses were conducted using *SPSS 16*®.

For the data available between 1994 and 2011, we examined the relationships between hospital cases of ciguatera poisoning and disturbance records using wavelet, cross-wavelet, and wavelet coherence analyses (Grinsted et al., 2004). All wavelet analyses were implemented using *Matlab 6.5*®. We were interested in determining whether there was: (i) any periodic cycling within each time series, (ii) any common power between the two time series, and (iii) any phase relationship and coherence between the two time series (Grinsted et al., 2004).

3. Results

3.1. Reef state from 1970 to 2011

The reefs of Rarotonga have experienced several large disturbances over the last four decades (Table 1). Four tropical cyclones of Category 3 and lower (i.e., cyclones, storms, and gales) impacted Rarotonga in the 1970s (see Table 1). In 1971, Devaney and Randall (1973) reported the first known *A. planci* outbreak in Rarotonga, which lasted until 1976. The sea stars reduced hard coral cover in the lagoon, although coral cover had recovered to pre-*A. planci* conditions by the late 1980s (G. Paulay, pers. comm.). In 1987, a Category 5 cyclone impacted Rarotonga, and from 1989 to 2001 seven Category 3 and lower storms impacted the reefs (see Table 1). Coral bleaching was first reported in 1991 in Rarotonga, when extreme low tides affected lagoon corals (Goreau and Hayes, 1995). Similar but less severe bleaching was observed on the reef crest in 1998, 2006, and 2009 (T. Rongo, pers. obs.; Rongo et al., 2009a). Coral bleaching, caused by high sea surface temperatures, was observed in 1994, but damage was limited to fore-reef corals (Goreau and Hayes, 1995). A second *A. planci* outbreak occurred from 1995 to 2001, where hard coral cover declined from an average of ~31% in 1994 (Miller et al., 1994) to ~5% in 2003 (Lyon, 2003) (Fig. 2a). Hard coral cover further declined to 1% in 2006, after six major cyclones impacted Rarotonga between 2003 and 2005 (Rongo et al., 2006). By 2009, however, hard coral cover had significantly increased to an average of 5% (Rongo et al., 2009a), and to an average of 8% by 2011 ($\chi^2 = 64$, $p < 0.001$) (Table 2).

3.2. Algae and herbivorous fishes

From 2006 to 2011, turf algal cover significantly declined ($\chi^2 = 55$, $p < 0.001$) (Fig. 2b; see Table 2), macroalgal cover significantly increased ($\chi^2 = 9$, $p = 0.01$) (Fig. 2c; see Table 2), and acanthurid density significantly declined over the same time period ($\chi^2 = 18$, $p < 0.001$) (Fig. 3; Table 3). The algal turf grazer *A. nigrofuscus* was the most common acanthurid at all sites; other acanthurids were recorded infrequently. The average density of the detritivore *C. striatus* significantly declined ($\chi^2 = 46$, $p < 0.001$) from

Table 1
Natural disturbances (including cyclones, crown-of-thorns starfish outbreaks, and coral bleaching) impacting Rarotonga, Cook Islands, between 1970 and 2011. Cyclone and wind data taken from Asian Development Bank (2005), de Scally et al. (2006), Baldi et al. (2009), and New Zealand's National Institute of Water and Atmospheric Research database (www.cliflo.niwa.co.nz). Cyclone, storm, and gale refer to Category ≤3 systems, and major cyclones refer to Category 4 and 5 systems. Wind speeds reported here are those noted for Rarotonga. *Acanthaster planci* outbreak data and coral bleaching information were taken from Devaney and Randall (1973), Goreau and Hayes (1995), Lyon (2003), Rongo et al. (2006, 2009a), and Rongo and van Woesik (2011). Severity factor is based on the damage noted in Rarotonga from 1994 to 2011, with 5 being the most severe. SST refers to sea surface temperature.

Year	Natural disturbance	Severity factor	Description of impact
1970	*Acanthaster planci* outbreak begins; Cyclone (Dolly)		*Dolly*: high winds damaged ~40% of Rarotonga's export banana crop; information on wave damage not available
1971	*A. planci* outbreak		
1972	*A. planci* outbreak; Cyclone (Agatha)		Extensive damage from *A. planci* outbreak noted in lagoon areas on the northwestern exposure; *Agatha*: wind speeds up to 134 km/h that damaged ~75% of Rarotonga's export banana crop; information on wave damage not available
1973	*A. planci* outbreak		
1974	*A. planci* outbreak		
1975	*A. planci* outbreak		
1976	*A. planci* outbreak ends; Storm (Kim)		Lagoon coral cover declined from *A. planci* outbreak; *Kim*: wind speeds up to 135 km/h, causing some fishing vessel damage
1978	Cyclone (Charles)		*Charles*: wind speeds up to 135 km/h; wave height of 11 m; reported to have caused damage to the wharf
1987	Major cyclone (Sally)		*Sally*: wind speeds up to 156 km/h and wave height of 12 m
1989	Gale (unnamed)		*Gale*: wind speeds up to 105 km/h; no information on swells
1991	Cyclone (Val); Coral bleaching		*Val*: wind speeds up to 74 km/h and wave height of 14 m; severe bleaching of lagoon corals from extreme low tides
1992	Cyclone (Gene)		*Gene*: wind speeds up to 115 km/h; flooding and big swells with coastal damage on western exposure
1993	Cyclone (Nisha)		*Nisha*: wind speeds up to 74 km/h; big swells
1994	Coral bleaching	1	Coral bleaching from high SSTs impacted corals on fore reef slopes on the northern to western exposure
1995	*A. planci* outbreak begins	3	Large numbers noted on the northern fore reef exposure
1996	*A. planci* outbreak	4	Extensive damage of fore reef slopes on the northern exposure
1997	Cyclone (Pam); *A. planci* outbreak	5	*Pam*: wind speeds up to 150 km/h; wave height of 14 m; record rainfall of 107 mm in 6 h; *A. planci* damage on the northeastern exposure
1998	*A. planci* outbreak; Coral bleaching	3	*A. planci* damage on eastern and southeastern exposure; coral bleaching of lagoon corals from extreme low tides
1999	*A. planci* outbreak	2	Extensive damage of fore reef slopes on the southern exposure
2000	*A. planci* outbreak	2	Extensive damage of fore reef slopes on the southwestern and western exposure
2001	*A. planci* outbreak ends; Storms (Oma, Trina)	4	*A. planci* outbreak significantly reduced fore reef coral cover; *Oma*: wind speeds up to 130 km/h and heavy rain; *Trina*: wind speeds up to 102 km/h with big swells
2002		0	
2003	Major cyclone (Dovi); Titikaveka Irritant Syndrome (TIS)	5	*Dovi*: wind speeds up to 66 km/h and wave height of 17 m; strong swell/surge along coastal areas; *TIS*: harmful algal bloom causing eye and respiratory irritation in residents
2004	Major cyclone (Heta)	5	*Heta*: wind speeds up to 72 km/h and wave height of 17.4 m; major coastal damage
2005	Major cyclones (Meena, Nancy, Olaf, Percy); Gale (Rae)	5	Severe coastal damage from the four major cyclones; *Meena*: wind speeds up to 161 km/h and wave height of 17 m; *Nancy*: wind speeds up to 165 km/h and wave height of 22 m; *Olaf*: wind speeds up to 95 km/h and wave height of 16 m; *Percy*: wind speeds up to 76 km/h and wave height of 19 m; *Rae*: wind speeds up to 75 km/h
2006	Coral bleaching	1	Coral bleaching of lagoon corals observed in Ngatangiia on the southeastern exposure from extreme low tides
2007		0	
2008		0	
2009	Coral bleaching	1	Minor bleaching observed on reef flats on the northern exposure from extreme low tides
2010		0	
2011		0	

2006 to 2011 (see Fig. 3; see Table 3). The average density of the scraping, herbivorous parrotfishes, particularly *Chlorurus frontalis*, *C. sordidus*, *Scarus altipinnis*, *S. schlegeli*, and *S. psittacus*, did not differ over time ($\chi^2 = 0.1$, $p = 0.95$) (see Fig. 3; see Table 3).

3.3. Relationship between ciguatera and disturbances

The wavelet analyses of reef disturbances and cases of ciguatera poisoning, from 1994 to 2011, both showed 4- to 5-year return periods (Fig. 4a). Indeed, the cross-wavelet analysis showed common power at the 4-year period, with a relative in-phase relationship (i.e., arrows to the right; Fig. 4b) between disturbances and cases of ciguatera. The wavelet-coherence analysis indicated a significant in-phase relationship between disturbances and cases of ciguatera, particularly from 2000 to 2005 (Fig. 4c).

4. Discussion

Although a minor outbreak of ciguatera poisoning occurred in the early 1970s in Rarotonga, it was not until

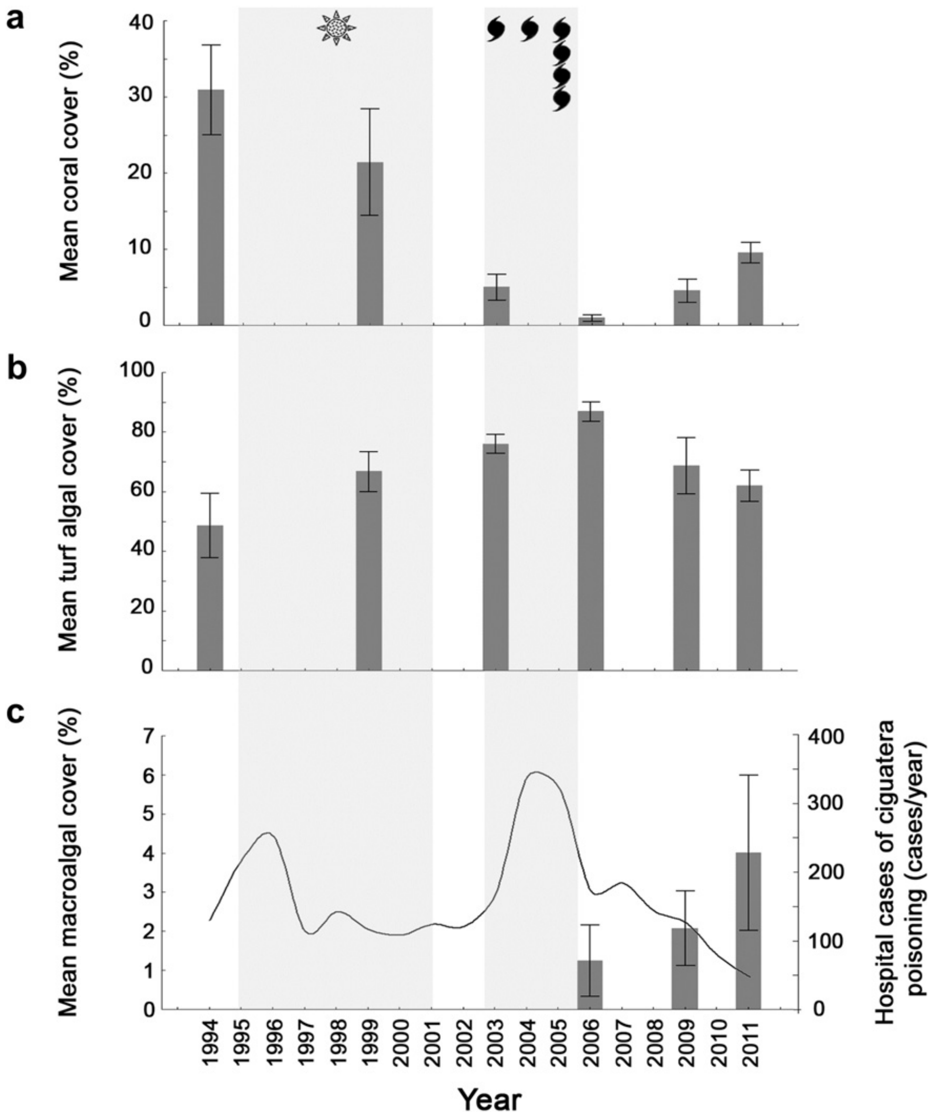

Fig. 2. (a) Mean hard coral (%), (b) mean turf algal cover (%), and (c) mean macroalgal cover (%) on fore reef sites of Rarotonga, Cook Islands in 1994 (Miller et al., 1994), 1999 (Ponia et al., 1999), 2003 (Lyon, 2003), 2006 (Rongo et al., 2006), 2009 (Rongo et al., 2009a), and 2011. The black line in figure (c) indicates the number of hospital cases of ciguatera poisoning per year in Rarotonga from 1994 to 2011 (August). Shaded areas indicate the *Acanthaster planci* (star symbol) outbreak between 1995 and 2001, and major cyclones (Category 4 or 5; black symbols) that impacted Rarotonga between 2003 and 2005. Error bars represent 95% confidence intervals.

Table 2
The mean percentage cover of hard corals, turf algae, and macroalgae (±standard error) at Rarotonga, Cook Islands, fore-reef sites surveyed in 1994 (Miller et al., 1994), 1999 (Ponia et al., 1999), 2003 (Lyon, 2003), 2006 (Rongo et al., 2006), 2009 (Rongo et al., 2009a), and 2011. A Friedman test was used to examine differences in the biological parameters of interest among years (2006, 2009, and 2011; gray shaded area).

Year	Hard coral (mean %)	Turf algae (mean %)	Macroalgae (mean %)
1994	31 ± 3	49 ± 5	
1999	21 ± 3	66 ± 3	
2003	5 ± 1	76 ± 1	
2006	1 ± 0.2	87 ± 2	1 ± 0.5
2009	5 ± 1	69 ± 5	2 ± 0.5
2011	8 ± 1	62 ± 4	4 ± 1
Friedman test	$\chi^2 = 64$, $p < 0.001$	$\chi^2 = 55$, $p < 0.001$	$\chi^2 = 9$, $p = 0.01$

the 1990s when ciguatera poisoning became severe (Rongo et al., 2009b; Rongo and van Woesik, 2011). From 1991 to 2005, Rarotonga experienced, on average, one major reef disturbance per year (see Table 1), which coincided with the highest incidence of ciguatera poisoning reported in the literature. The wavelet analysis showed an in-phase relationship between reef disturbances and ciguatera cases from 1994 to 2011 (see Fig. 4c); ciguatera cases increased with increased severity of disturbance. Ciguatera cases and disturbances showed a return period of four years (see Fig. 4b), which also coincides with the inter-annual cycle of the El Niño Southern Oscillation (ENSO).

Although our wavelet analysis showed a direct in-phase relationship between reef disturbances and ciguatera cases, we did not undertake a wavelet lag coherence analysis to check for any lag period between disturbances and cases. However, in our previous work from Rarotonga (see Rongo and van Woesik, 2011), we showed a one- to two-year lag

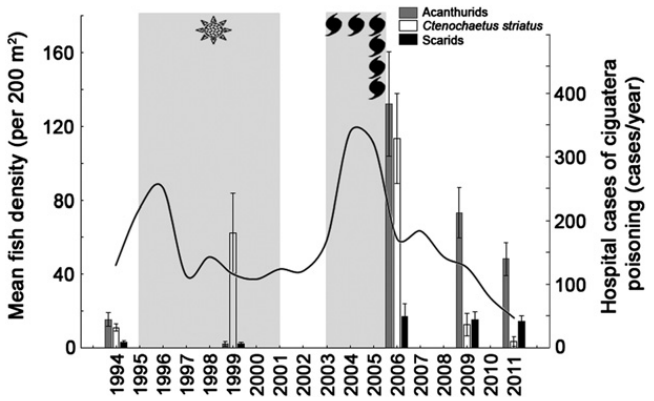

Fig. 3. Hospital cases of ciguatera poisoning in Rarotonga per year (represented by the black line) from 1994 to 2011 (August), and mean fish density (per 200 m^2) in 1994 (Miller et al., 1994), 1999 (Ponia et al., 1999), 2006 (Rongo et al., 2006), 2009 (Rongo et al., 2009a), and 2011. Shaded areas indicate the *Acanthaster planci* (star symbol) outbreak between 1995/96 and 2001, and major cyclones (Category 4 or 5; black symbols) that impacted Rarotonga between 2003 and 2005. Error bars represent 95% confidence intervals.

period between an increase in ciguatera cases during the negative ENSO phase (or El Niño) when cyclone frequency was higher than during the positive ENSO phase (or La Niña; see de Scally, 2008). This lag period was consistent with other studies in the Pacific. For example, Chateau-Degat et al. (2005) showed a lag period of 16–20 months between peaks of elevated sea water temperature and ciguatera poisoning in French Polynesia. In addition, Kaly and Jones (1994) showed a one-year lag period between peak densities of *Gambierdiscus toxicus* and peak toxicity in herbivorous reef fishes in Tuvalu.

This study showed evidence of an increase in the density of herbivorous and detritivorous reef fishes after the passing of major cyclones, particularly between 2003 and 2005 (see Fig. 3). Such increases in herbivorous fish densities have been shown to be a consequence of increased algal cover after the loss of corals (Sheppard et al., 2002; Wilson et al., 2006). An increase in the densities of these fishes may have increased the probability of ciguatoxin transfer (Fig. 5). In support, the increased density of the detritivore *C. striatus* directly coincided with increased

Table 3
Mean density (per 200 m^2) of acanthurids, *Ctenochaetus striatus*, and scarids (±standard error) at fore reef sites Rarotonga, Cook Islands, surveyed in 1994 (Miller et al., 1994), 1999 (Ponia et al., 1999), 2006 (Rongo et al., 2006), 2009 (Rongo et al., 2009a), and 2011. A Friedman test was used to examine differences among years (2006, 2009, and 2011; gray shaded area).

Year	Acanthurids (mean density per 200 m^2)	*Ctenochaetus striatus* (mean density per 200 m^2)	Scarids (mean density per 200 m^2)
1994	15 ± 2	11 ± 1	3 ± 1
1999	2 ± 1	62 ± 11	2 ± 1
2006	133 ± 14	113 ± 12	17 ± 3
2009	73 ± 7	13 ± 3	15 ± 2
2011	46 ± 5	4 ± 2	14 ± 2
Friedman test	$\chi^2 = 18$, $p < 0.001$	$\chi^2 = 46$, $p < 0.001$	$\chi^2 = 0.1$, $p = 0.95$

hospital cases of ciguatera poisoning. Similarly, the density of *C. striatus* significantly declined in 2009 and later, directly coinciding with the decline in hospital cases of ciguatera poisoning that in 2011 were the lowest in 20 years (see Fig. 3).

The contribution of *C. striatus* in algal removal is arguably limited, as the species was thought to be essentially a detritivore (e.g., Choat et al., 2004; Green and Bellwood, 2009). However, a recent study by Marshell and Mumby (2012) showed that *C. striatus* removed considerably more turf algae than previously thought. Interestingly, Marshell and Mumby (2012) also found that *A. nigrofuscus* (the most common herbivore in our second category) was also an important grazer of turf algae, and was therefore a potential vector for ciguatoxins.

In addition to the effect of increased densities of herbivorous reef fishes following reef disturbance events, we suggest that there is also a potentially cascading societal effect of ciguatera. The fear of ciguatera poisoning among residents in Rarotonga caused a decline in fishing activities through the 1990s (Solomona et al., 2009) that has continued to the present day (Rongo and van Woesik, 2012). This societal behavioral change also effectively generated a natural marine protected area that contributed to increased fish densities, which in turn escalated the potential for the transfer of ciguatoxins into the food web (see Fig. 5). Differences in fishing pressure may explain why herbivorous fish densities were lower in 1994 compared with 2006 (see Fig. 3), despite reef disturbances occurring during both periods (see Table 1). In addition, low fish densities in 1994 may explain why the upsurge in hospital cases was lower during this period than the upsurge noted after 2003 when fish densities were high.

Since 2005, Rarotonga has not experienced a major cyclone, and ciguatera poisoning has simultaneously diminished. Cyclones in the southern Cook Islands are most active during El Niño years (de Scally, 2008), and El Niño events tend to be more frequent during the positive phase of the Pacific Decadal Oscillation (PDO) (Verdon and Franks, 2006). The PDO is the dominant climate cycle in the Cook Islands region (Linsley et al., 2000; Rongo et al., 2009b), fluctuating from a positive to a negative phase approximately every 30 years. The recent shift (in late 2008) of the PDO to the negative phase suggests that cyclone frequency and intensity will likely remain low in Rarotonga for the next decade or more, and the corals will most likely continue to recover (see Fig. 5).

From 2006 to 2011, the increase in coral cover matched a decline in cases of ciguatera poisoning. Nevertheless we do not suggest that coral cover (i.e., reef state) is a good indicator of the risk of ciguatera poisoning, because this study showed no such evidence. For example, coral cover in 1994 was greater than 20%, whereas in 2011 it was approximately 8%, yet cases of ciguatera poisoning were higher in 1994 than in 2011. We do however suggest that the disturbances to the reefs instigate the outbreak of opportunistic, ciguatoxic dinoflagellate populations. It seems that large waves associated with cyclones reset algal succession, facilitating the colonization of opportunistic ciguatoxic dinoflagellates, thereby increasing the risk of ciguatera poisoning.

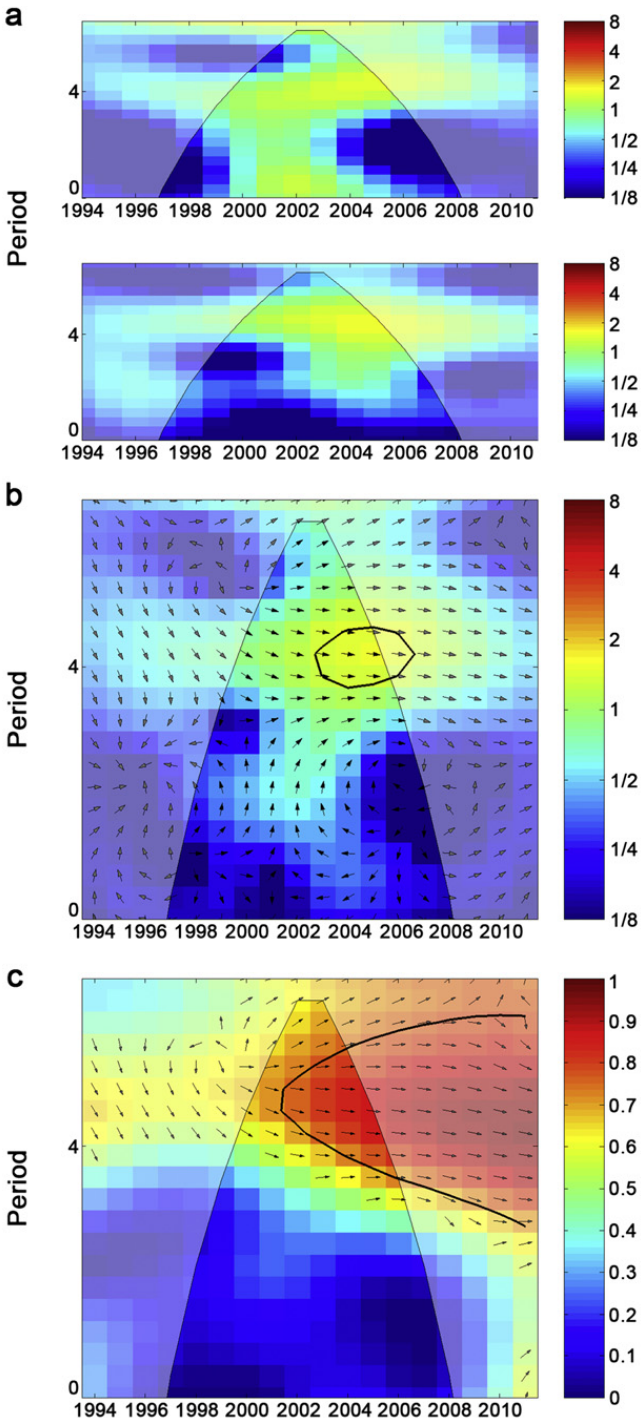

Fig. 4. (a) Wavelet analysis of the reef disturbance categories (*top*) and yearly Rarotonga hospital cases of ciguatera poisoning (*bottom*) from 1994 to 2011 (August). (b) Cross wavelet transformation of reef disturbances and cases of ciguatera poisoning. (c) Wavelet-coherence analysis of reef disturbances and cases of ciguatera poisoning. The black line depicts the cone of influence in each subplot, and the thick, black line contour in (b) and (c) designates the 5% significance level against red noise. We note that arrows to the right denote an in-phase relationship, arrows to the left denote an anti-phase relationship, and arrows straight up or down indicate an out-of-phase relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Often the most common algae on reefs are unpalatable to herbivorous fishes. In Rarotonga, these unpalatable algae have been primarily *Galaxaura* spp. (a calcified alga) and *Asparagopsis taxiformis* (a chemically-defended alga) (see Cruz-Rivera and Villareal, 2006). While these algae were present at the survey sites, which were between 7 and 9 m, they were considerably more abundant $\leq$5 m, making them particularly vulnerable to storm damage. Major cyclones appear to remove these unpalatable algae (e.g., Andres and Witman, 1995), which then lead to a successional increase in palatable algae. Other studies support these conjectures. For example, several studies have suggested that early successional, opportunistic turf algae have high nutrient content and are more palatable than late

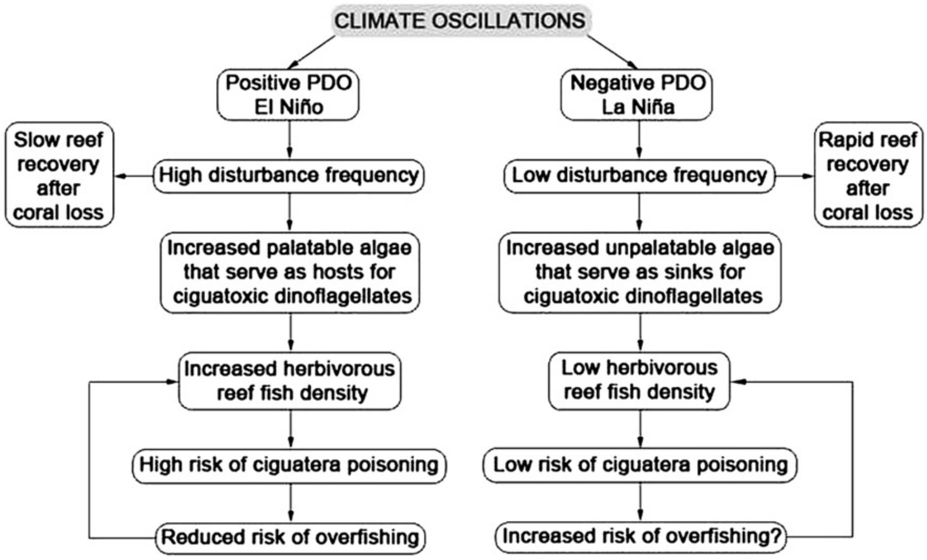

Fig. 5. Schematic depiction of the suggested influence of climate oscillations on ciguatera poisoning in Rarotonga, Cook Islands. The positive phase of the Pacific Decadal Oscillation (PDO) is coupled with El Niño years, whereas the negative phase of the PDO is coupled with La Niña years. Disturbance frequency refers to cyclones and coral bleaching events that can impact coral reefs by reducing coral cover, and by creating new surfaces for macroalgae and opportunistic dinoflagellates. Herbivorous fishes refer to the primary vectors of ciguatoxins, such as acanthurids (primarily *Ctenochaetus striatus*) and scarids. Under a climate phase with a high risk of ciguatera poisoning, reduced fishing pressure would form a natural marine protected area leading to increases in herbivorous fish density. Alternatively, under a climate phase with low risk of ciguatera poisoning, Rarotongans tend to return to a reef fish diet and thus the risk of overfishing is increased – highlighting the need for the maintenance of the Rarotongan *ra'ui* (Marine Protected Areas).

successional algae (e.g., Littler and Littler, 1980; Steneck and Dethier, 1994). The increased cover of opportunistic turf algae (an important host for ciguatoxic dinoflagellates; see Cruz-Rivera and Villareal, 2006) after the 2003–2005 cyclones, increased the likelihood of ciguatoxin transfer into the food web by herbivorous fishes (see Fig. 5). The absence of cyclone activity since 2005 may explain the increased cover of unpalatable macroalgae and the decreased cover of turf algae (see Fig. 2), which may have consequently contributed to the recent decline of herbivorous fish densities.

In conclusion, we found that a high frequency of reef disturbance preceded increased densities of herbivorous reef fishes, especially those fishes important in the transfer of ciguatoxins into the food web. Similarly, cases of ciguatera poisoning declined in synchrony with declines in the densities of herbivorous reef fishes. This study also showed that coral cover is not a good predictor of ciguatera poisoning, but that high cyclone activity was a good predictor of ciguatera. High cyclone activity coincided with El Niño years, which were most prevalent during the positive phase of the PDO. The recent shift in climate oscillations to the negative phase of the PDO, coupled with La Niña years (when Rarotonga experiences fewer cyclones), suggests that cyclones will remain infrequent for the next decade or more. We predict that fewer cyclones will sequester the intensity of ciguatera poisoning and may also give the coral populations on the reefs a chance to recover.

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Conflict of interest

We have no conflicts of interest to disclose.

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