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Hurricanes and coral bleaching linked to changes in coral recruitment in Tobago

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ABSTRACT

Knowledge of coral recruitment patterns helps us understand how reefs react following major disturbances and provides us with an early warning system for predicting future reef health problems. We have reconstructed and interpreted historical and modern-day recruitment patterns, using a combination of growth modelling and in situ recruitment experiments, in order to understand how hurricanes, storms and bleaching events have influenced coral recruitment on the Caribbean coastline of Tobago. Whilst Tobago does not lie within the main hurricane belt results indicate that regional hurricane events negatively impact coral recruitment patterns in the Southern Caribbean. In years following hurricanes, tropical storms and bleaching events, coral recruitment was reduced when compared to normal years ($p = 0.016$). Following Hurricane Ivan in 2004 and the 2005–2006 bleaching event, coral recruitment was markedly limited with only 2% ($n = 6$) of colonies estimated to have recruited during 2006 and 2007. Our experimental results indicate that despite multiple large-scale disturbances corals are still recruiting on Tobago's marginal reef systems, albeit in low numbers.

1. Introduction

An increasing amount of evidence is now accumulating for a direct relationship between global warming and increasing hurricane intensity as well as increasing hurricane frequency (Elsner et al., 2006a,b). Global warming produces significant increases in the frequency of high sea surface temperatures (SSTs) (Hoegh-Guldberg, 1999; Crabbe et al., 2008a), and hurricane winds are strengthened by warm surface waters. Maintaining coral reef populations in the face of large-scale degradation and phase-shifts on reefs depends critically on recruitment (Hughes and Tanner, 2000; Coles and Brown, 2007), and the present study set out to test the hypothesis that hurricanes, tropical storms and bleaching events limit the recruitment and subsequent survival of massive non-branching corals. While healthy reefs usually have high numbers of coral recruits and juvenile corals, degraded systems typically have limited numbers of young colonies (Meesters et al., 2001; Smith et al., 2005). An understanding of population dynamics and coral recruitment patterns helps in understanding how reefs react following major disturbances and provides us with an early warning system for predicting future reef health problems. Physical (e.g. sedimentation, salinity, temperature, wave energy, substrate availability) and biological (e.g. predation, density and size of adult colonies, reproductive strategy) factors influence coral reproduction and subsequent recruitment levels (Loya, 1976; Cortes and Risk, 1985; Szmant, 1986; Gilmour, 1999; Crabbe et al., 2002; Vermeij et al., 2006). Coral bleaching, the loss of colour in the dinoflagellate algae (genus: *Symbiodinium*) and the coral host, is considered highly deleterious to coral health having negative impacts on growth and reproduction, and making colonies more susceptible to mechanical damage, disease and mortality (Douglas, 2003). A number of external factors can trigger bleaching including elevated temperature, sediment smothering, reduced salinity, increased ultra-violet irradiation (Abrego et al., 2008).

We have shown previously that growth modelling indicated that hurricanes and severe storms were linked to low coral recruitment in the Caribbean, on the fringing reefs of the north coast of Jamaica near Discovery Bay (Crabbe et al., 2002), and on the barrier reef and patch reefs off the coast of Belize (Crabbe et al., 2008b). We wished to test that hypothesis further and assess whether patterns of coral recruitment in Tobago have been influenced by recent extreme climate-driven events: hurricanes, tropical storms and temperature-induced coral bleaching. Whilst Tobago does not fall within the main hurricane belt the effects of passing storms and hurricanes still influences the island. Hurricanes and storms result in increased rainfall, severe flooding and high levels of terrestrial runoff. High wave energy causes coastal erosion, sediment scouring, mechanical breakage, redistribution of clasts, and loss of substrate. These effects can result in severe damage, or subsequent

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mortality, to coral colonies and loss of suitable substrate for colonisation (Knowlton et al., 1981; Connell, 1997; Connell et al., 1997). The most recent bleaching event in Tobago was temperature-induced, beginning in September 2005 and lasting until mid-2006, and affected ⩾66% of Tobago's corals (O'Farrel and Day, 2005). Many colonies subsequently died (7%) or suffered from partial mortality (33%), whilst the prevalence of coral diseases, especially on the main framework builders *Montastrea faveolata*, increased (Bouchon et al., 2008a,b; Mallela and Parkinson, 2008).

In this study we have reconstructed and interpreted historical and modern-day recruitment patterns, using a combination of growth modelling and in situ coral recruitment experiments, in order to understand how hurricanes, storms and bleaching events have influenced coral recruitment on Tobago's reefs.

2. Materials and methods

2.1. Study sites

Tobago represents the southern most extreme for modern-day framework building coral reefs in the Caribbean. The reefs are characterised by seasonal pulses of river discharge from South America, in particular the Orinoco River during the rainy season (June–December). Riverine inputs include freshwater, sediments and nutrients which result in sub-optimal reef building conditions during the wet season (Bouchon et al., 2008b; Mallela and Harrod, 2008). As a result Tobago's reefs have evolved, developed and adapted to wide ranging environmental fluctuations which include seasonal pulses of acute, riverine disturbance. For example, in 2008 at a depth of 10 m, data obtained from in situ Star-Oddi™ data loggers revealed that salinity ranged from 11.2 to 36.1; temperature ranged from 22.1 to 30.3 °C, and sedimentation rates at 10 m depth in 2007 ranged from 0.3 to 15.9 mg cm^{-2} d^{-1}.

Six reef locations: Kariwak, Buccoo, Mt. Irvine, Culloden, Little Englishman's Bay and Sisters, were selected along the Caribbean coastline of Tobago (Fig. 1). At each site, at a depth of 10 m, historical and recent coral recruitment patterns were determined using a combination of methods which included: (1) growth modelling of in situ colonies, and (2) artificial settlement plates to assess rates of coral recruitment.

2.2. Growth modelling

Permanent monitoring transects were established at each site at a depth of 10 m. In May and October 2008 coral colonies were haphazardly selected along the transect lines whilst SCUBA diving. The surface area of living, non-branching, scleractinian corals was determined using a series of in situ measurements. The largest diameter of each colony was measured using a vinyl tape measure, the diameter at 90° to that, and the total circumference of the colony. Colonies that were close together, touching, showed signs of partial mortality, fission or fusion were avoided to minimise age discontinuities (Hughes and Jackson, 1980). A total of 354 colonies were measured and ages subsequently estimated using known growth rates modified where appropriate using a rational polynomial function (RPF) (Carricart-Ganivet et al., 2000; Huston, 1985; Crabbe et al., 2002, 2008b; Crabbe and Smith, 2005; Bardsley, 2009).

The year of an individual's recruitment was estimated using the RPF growth model which was based on knowledge of pre-existing growth rate literature (e.g. 3.25 mm $year^{-1}$ for *Porites astreoides*, 3 mm $year^{-1}$ for *Siderastrea siderea*) (Dodge and Vaisnys, 1975; Hubbard and Scaturo, 1985; Huston, 1985; Carricart-Ganivet et al., 2000). Data was taken from sites in the Caribbean at similar depths and visibility to those encountered here, the majority from Huston (1985). For example, a *P. astreoides* colony of measured elliptical surface area 51.8 cm^2 was estimated to have recruited (and survived) 23 years ago. The modelled changes to the growth rates were similar to those encountered at different sites and similar depths from the references above, and in none of the colonies studied did error levels amount to >10% of the growth rates measured, equating to a change in estimated recruitment date of <±2 years. One or two-factor ANOVA was used to compare coral data among sites; ±error values represent standard deviations of the data unless otherwise stated.

2.3. Settlement plates

Prior studies indicate that ceramic settlement plates can be used to accurately assess coral and encruster recruitment (Mallela, 2007; Mallela and Perry, 2007). In May 2007, ceramic settlement plates (locally made, unglazed clay: surface area 81 cm^2) were

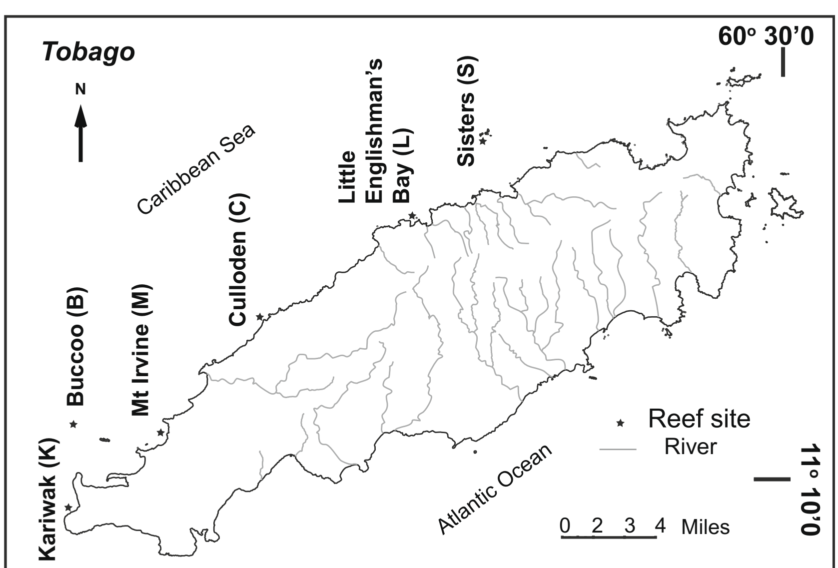

Fig. 1. Map of Tobago, showing the six reef locations selected along the Caribbean coastline of Tobago in this study: Kariwak, Buccoo, Mt. Irvine, Culloden, Little Englishman's Bay and Sisters.

placed at 10 m on six reefs in Tobago: Kariwak, Buccoo Reef, Mt. Irvine, Culloden, Little Englishman's Bay and Sisters Rocks. Plates were positioned in three orientations in order to mimic natural substrate conditions: exposed/upwards facing (e), cryptic/downwards facing (c), and vertically (v). Eighteen plates (six orientation^{-1}) were lifted from each site after 6 months and 12 months. Twelve month settlement plates were lost at Sisters due to extreme weather conditions. All tiles were screened for coral recruits using a binocular microscope.

3. Results

Our results indicate that despite multiple large-scale disturbances corals are still recruiting on Tobago's marginal reef systems, albeit in low numbers. Fig. 2 shows the modelled recruitment year for colonies that have recruited to Tobago's reefs since 1980. We identified hurricane, storm and bleaching events which were reported to have had an impact on Tobago's reefs, these included: coral bleaching (2005–2006), Hurricane Ivan (2004), Tropical Storm Isidore (2002), Tropical Storm Bret (1993), and Tropical Storm Danielle (1986). In the early 1980s numbers of the grazing urchin, *Diadema antillarum*, plummeted in Tobago due to a Caribbean wide disease outbreak. There were also wide spread Caribbean bleaching events in 1980, 1983, 1990 and 1995, however we were unable to find any records or reports of this in Tobago, consequently these years were not considered bleaching years in our analyses (Fig. 2). The results presented here therefore focus on a 25 year period from 1983 to 2008 on events with reliable records of environmental disturbances on Tobago's reefs. Years where there were no reported effects of hurricanes, storms or bleaching are from here-in referred to as 'normal' or 'non-event' years.

3.1. Growth modelling

Between 1983 and 2006 we identified several distinct hurricane, tropical storm and bleaching events (Fig. 2), 290 of our colonies also recruited during this period. At all sites, results indicate that in years following hurricanes, tropical storms and bleaching events coral recruitment was significantly limited when compared to normal years, (One-way ANOVA: $F = 6.8$, $p = 0.016$, Figs. 2 and 3). The peak period for successful recruitment for coral colonies in Tobago occurred between 1999 and 2001, following six normal years, this three year period accounted for 28% of coral colony recruitment since 1983. Following Hurricane Ivan in 2004 and the 2005–2006 bleaching event coral recruitment on Tobago's reefs was severely limited with only 2% ($n = 6$) of our colonies estimated to have recruited during 2006 and 2007.

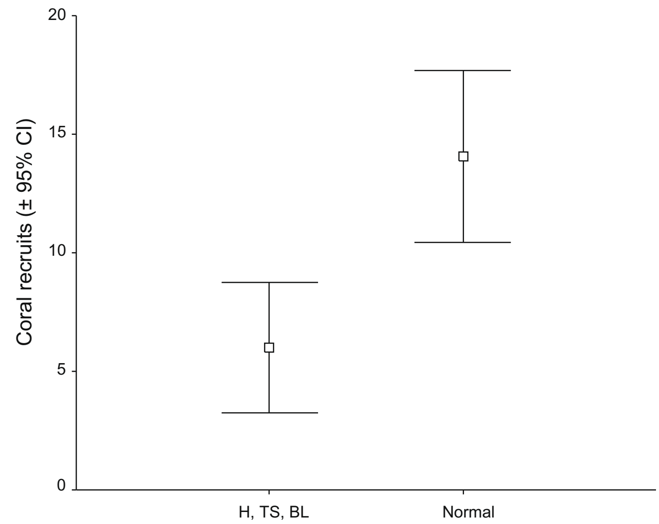

Fig. 3. Mean number (±95% confidence intervals) of coral colonies recruiting in hurricane (H), tropical storm (TS) and bleaching (BL) years ($n = 6$) versus normal years with no reported incidents ($n = 18$), 1983–2006.

A total of 18 species had recruited since 1983, dominant species included: *Colpophyllia natans* (3% of all colonies), *Diploria labyrinthiformis* (10%), *Diploria strigosa* (28%), *Montastrea cavernosa* (11%), *M. faveolata* (17%), *P. astreoides* (9%) and *S. siderea* (10%) (Fig. 2). However, following the 2005–2006 bleaching event we observed a distinct drop in the numbers (Figs. 2 and 3) and biodiversity (Fig. 2) of coral recruits at all sites with only four species present: *C. natans, D. strigosa, Favia fragum,* and *Meandrina meandrites.* All sites displayed similar patterns of reduction in coral recruitment following disturbance events.

3.2. Coral recruitment on settlement plates after the 2005 bleaching event

The number of recent, live recruits observed on settlement plates between 2007 and 2008 confirmed findings from our RPF modelling. Limited coral recruitment occurred after 6 and 12 months (Fig. 4) with a total of 12 ($n = 6$ sites) and 17 recruits ($n = 5$ sites) observed, respectively on all plates at all six sites. Buccoo had the most recruits after 12 months, with six recruits being observed on the 18 plates, all other sites had $\leqslant 3$ recruits

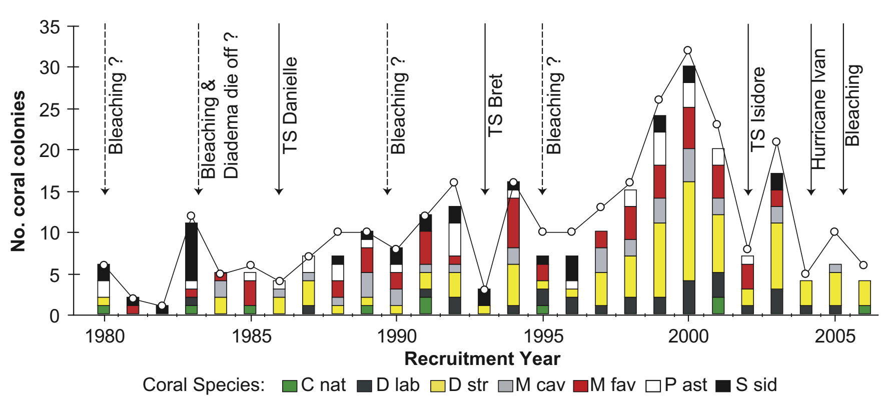

Fig. 2. The estimated year of recruitment for all coral colonies in this study 1980–2006 (solid black line), solid arrows indicate when hurricanes, tropical storms (TS) and bleaching events occurred. Dashed arrows indicate events which may have impacted Tobago's reefs but were not cited in records. The histogram underneath gives the estimated year of recruitment for dominant coral species: *Colpophyllia natans* (green), *Diploria labyrinthiformis* (dark grey), *Diploria strigosa* (yellow), *Montastrea cavernosa* (light grey), *Porites astreoides* (white), *Siderastrea siderea* (black). (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

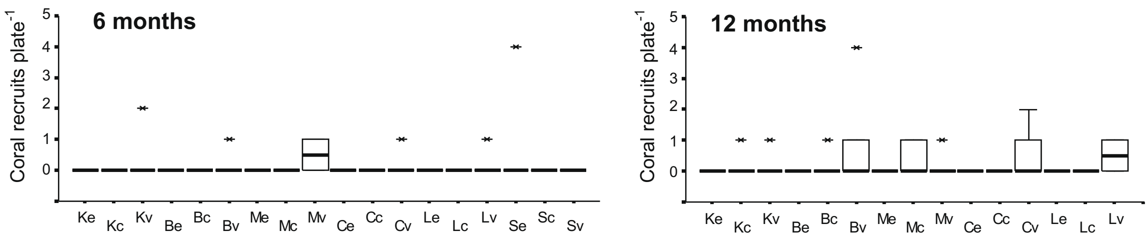

Fig. 4. Coral recruitment on settlement plates after the 2005 bleaching event. Box whisker plots detailing coral recruitment after 6 and 12 months on settlement plates at 10 m. Reef sites: Kariwak (K), Buccoo (B), Mt. Irvine (M), Culloden (C), Little Englishman's Bay (L), Sisters (S). Plates positioned in three orientations horizontal exposed (e), horizontal cryptic (c), vertical (v). Note 12 month tiles at Sisters were lost.

on plates after 12 months. Recruits showed a preference for vertical tiles ($n = 8$ and 13) after 6 and 12 months, respectively, with cryptic ($n = 0$ and 4) and exposed ($n = 4$ and 0) tiles showing limited recruitment. Sisters was the only site where recruits had a preference for exposed tiles ($n = 4$) after 6 months.

4. Discussion

Our growth modelling and settlement plate experiment indicate that coral recruitment declined significantly in years following hurricanes, tropical storms and coral bleaching events. Findings from the settlement plates suggest that recovery can be slow; in this case more than 2 year after the bleaching event Tobago's coral recruitment was still limited in terms of numbers and biodiversity. The main framework builder on Tobago's reefs at the time of this study was *M. faveolata* (Bouchon et al., 2008b), however the live coral cover of this species has fallen dramatically following the 2005 bleaching event and a subsequent disease outbreak of yellow band disease is impacting the remaining population (O'Farrel and Day, 2005; Bouchon et al., 2008a; Mallela and Parkinson, 2008). In this study, we did not observe recruitment of *M. faveolata* following the multiple disturbance effects of Hurricane Ivan (2004) and the 2005–2006 bleaching event. Limited numbers of juvenile *D. strigosa* and *C. natans* were observed to have successfully recruited post-bleaching. These findings could have implications for the future health of Tobago's reefs since the continued occurrence of a diverse range of recruits and juvenile corals is essential in ensuring healthy, resilient, framework building coral reefs (Smith et al., 2005).

Other studies on clear water reefs in the Caribbean have also assessed the effects of hurricanes, storms and bleaching on coral recruitment. In Jamaica, a reduction in coral recruitment of non-branching corals was linked to the effects of storm damage, where increasing storm severity was negatively correlated with coral recruitment (Crabbe et al., 2002). Jamaican non-branching coral recruitment took 1–2 years to return to pre-hurricane levels, and while there was a reduction in numbers of colonies in Jamaican sites in 2006, after the mass bleaching of 2005, there were subsequent increases in 2007 and 2008 (Crabbe, 2009). Reefs of North Jamaica exhibit more rapid recovery than we are currently witnessing on Tobago's reefs following the combined effects of Hurricane Ivan and coral bleaching.

In Belize, in 1998 coral populations simultaneously experienced a severe coral bleaching event and Hurricane Mitch. A study of coral recruits (Mumby, 1999) found that whilst bleaching alone had no effect on recruitment density or community structure, the combined effects resulted in a 20% reduction of pre-disturbance levels. In Belize only 1% of recruits showed even partial mortality during the 1998 bleaching event. In contrast 66% of Tobago's coral colonies suffered from bleaching, with an estimated 73% of *C. natans* and *Diploria* spp. dying (Bouchon et al., 2008a). In our study *Diploria* spp. dominated the limited number of recruits from 2004 to 2006, with *C. natans* also recruiting in 2006, indicating low levels of recovery for these framework building species. Subsequent growth modelling work in Southern Belize (Crabbe et al., 2008b) also confirm these findings with significantly lower coral recruitment being observed in storm and hurricane years.

An earlier quantitative study in Tobago (Laydoo, 1993) on vertical ceramic plates at 14 m in Buccoo reef recorded mean recruitment levels of 188 m^{-2} $year^{-1}$, this is higher than those observed in this study where coral settlement on vertical plates at Buccoo equated to 103 (±SD 81) m^{-2} $year^{-1}$. These observations suggest that 12–18 months after the bleaching event coral recruitment on Tobago's reefs was still limited when compared to recruitment levels in the early 1990s following a series of normal years. Our study also indicates that the majority of recruits showed a preference for vertical orientations, as opposed to horizontal substrates again highlighting the importance of maintaining rugose, varied and complex reef structures.

Coral reefs that have been undermined can loose their ability to adapt and regenerate (Adger et al., 2005; Crabbe et al., in press). Tobago's reefs historically represent some of the most unusual marginal reef systems in the world having successfully developed in the Southern extreme of the Caribbean under the influence of regional riverine influence from two of the world's largest rivers, the Amazon and Orinoco. However, these reefs are now facing a series of multiple disturbances simultaneously for the first time. These disturbances include human induced climate change, over fishing, limited herbivory, increased prevalence of coral diseases, pollution from local land-based runoff and deteriorating water quality (Bouchon et al., 2008a,b; Burke et al., 2008; Mallela and Parkinson, 2008; Mallela and Harrod, 2008). It is generally accepted that climate change is likely to increase the intensity of hurricanes, storms, bleaching and rainfall events in the region (Bates et al., 2008), the findings presented here suggest that this in turn may limit successful coral recruitment. Whilst many of the less impacted reefs surrounding the island are still in a coral-dominated state the findings presented here should act as an early warning for coral reef managers. The small numbers of juvenile corals and very limited successful coral recruitment in recent years indicate that Tobago's reefs are currently experiencing a decrease in health which could have long-term implications.

In conclusion, our results are in agreement with findings from other regions in the Caribbean, indicating that hurricanes, storms and bleaching events do have negative impacts on coral recruitment. Current climate change predictions suggest that the occurrence of such extreme climate-driven events will increase. In order to maintain healthy, resilient reefs we must maintain the integrity of all the various reef components.

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