Accepted Manuscript

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

J. Mallela, M.J.C. Crabbe

PII: S0141-1136(09)00065-8
DOI: [10.1016/j.marenvres.2009.06.001](https://doi.org/10.1016/j.marenvres.2009.06.001)
Reference: MERE 3342

To appear in: *Marine Environmental Research*

Received Date: 25 January 2009
Revised Date: 28 May 2009
Accepted Date: 1 June 2009

Please cite this article as: Mallela, J., Crabbe, M.J.C., Hurricanes and coral bleaching linked to changes in coral recruitment in Tobago, *Marine Environmental Research* (2009), doi: [10.1016/j.marenvres.2009.06.001](https://doi.org/10.1016/j.marenvres.2009.06.001)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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

2

3 J. Mallela ^{1,2*} and M.J.C. Crabbe ³

4

5 ¹ Department of Life Sciences, The University of the West Indies, St Augustine,
6 Trinidad and Tobago, The West Indies.

7 ² ARC Centre of Excellence for Coral Reef Studies, Research School of Earth
8 Sciences, Australian National University, Canberra,
9 ACT, Australia (present address).

10 ³ LIRANS Institute for Research in the Applied Natural Sciences, Faculty of Creative
11 Arts, Technologies and Science, University of Bedfordshire, Park Square, Luton, LU1
12 3JU, U.K

13

14 *Corresponding author: J. Mallela. Email: j_mallela@yahoo.com

15

16

17 **Keywords:** tropical storms, hurricanes, climate change, Caribbean, global warming,
18 coral growth, recruitment, river discharge

1

2 **Abstract**

3 Knowledge of coral recruitment patterns helps us understand how reefs react
4 following major disturbances and provides us with an early warning system for
5 predicting future reef health problems. We have reconstructed and interpreted
6 historical and modern-day recruitment patterns, using a combination of growth
7 modelling and in-situ recruitment experiments, in order to understand how hurricanes,
8 storms and bleaching events have influenced coral recruitment on the Caribbean
9 coastline of Tobago. Whilst Tobago does not lie within the main hurricane belt
10 results indicate that regional hurricane events negatively impact coral recruitment
11 patterns in the Southern Caribbean. In years following hurricanes, tropical storms and
12 bleaching events, coral recruitment was reduced when compared to normal years ($p =$
13 0.016). Following Hurricane Ivan in 2004 and the 2005-2006 bleaching event, coral
14 recruitment was markedly limited with only 2 % ($n = 6$) of colonies estimated to have
15 recruited during 2006 and 2007. Our experimental results indicate that despite
16 multiple large-scale disturbances corals are still recruiting on Tobago's marginal reef
17 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

1 of external factors can trigger bleaching including elevated temperature, sediment
2 smothering, reduced salinity, increased ultra-violet irradiation (Abrego et al., 2008).

3 We have shown previously that growth modelling indicated that hurricanes
4 and severe storms were linked to low coral recruitment in the Caribbean, on the
5 fringing reefs of the north coast of Jamaica near Discovery Bay (Crabbe et al., 2002),
6 and on the barrier reef and patch reefs off the coast of Belize (Crabbe et al., 2008b).
7 We wished to test that hypothesis further and assess whether patterns of coral
8 recruitment in Tobago have been influenced by recent extreme climate-driven events:
9 hurricanes, tropical storms and temperature-induced coral bleaching. Whilst Tobago
10 does not fall within the main hurricane belt the effects of passing storms and
11 hurricanes still influences the island. Hurricanes and storms result in increased
12 rainfall, severe flooding and high levels of terrestrial runoff. High wave energy causes
13 coastal erosion, sediment scouring, mechanical breakage, redistribution of clasts, and
14 loss of substrate. These effects can result in severe damage, or subsequent mortality,
15 to coral colonies and loss of suitable substrate for colonisation (Knowlton et al. 1981;
16 Connell 1997; Connell et al. 1997). The most recent bleaching event in Tobago was
17 temperature-induced, beginning in September 2005 and lasting until mid-2006, and
18 affected $\geq 66\%$ of Tobago's corals (O'Farrel and Day 2005). Many colonies
19 subsequently died (7%) or suffered from partial mortality (33%), whilst the
20 prevalence of coral diseases, especially on the main framework builders *Montastrea*
21 *faveolata*, increased (Bouchon et al. 2008a and b; Mallela and Parkinson 2008).

22 In this study we have reconstructed and interpreted historical and modern-day
23 recruitment patterns, using a combination of growth modelling and in-situ coral
24 recruitment experiments, in order to understand how hurricanes, storms and bleaching
25 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 to 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 10m, data obtained from in-situ Star-OddiTM 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 10m 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 (Figure 1). At each site, at a depth of 10m, 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 10m. 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; Crabbe and Smith 2005; Crabbe et al. 2008b; 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 y⁻¹ for *Porites astreoides*, 3 mm y⁻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 cm² 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 cm²) were placed at 10m on 6 reefs in Tobago: Kariwak, Buccoo Reef, Mt Irvine, Culloden, Little Englishman's Bay and Sisters Rocks. Plates were positioned in 3 orientations in order to mimic natural substrate conditions: exposed / upwards facing (e), cryptic / downwards facing (c), and vertically (v). 18 plates (6 orientation⁻¹) were lifted from each site after 6 months and 12 months. 12 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. Figure 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 1980's 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 (Figure 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 (Figure 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: $F = 6.8$, $p = 0.016$, Figures 2 and 3). The peak period for successful recruitment for coral colonies in Tobago occurred between 1999-2001, 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.

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%) (Figure 2). However, following the 2005-2006 bleaching event we observed a distinct drop in the numbers (Figures 2-3) and biodiversity (Figure 2) of coral recruits at all sites with only 4 species present: *C. natans*, *D. strigosa*, *Favia fragum*, and *Meandrina meandrites*. All sites displayed similar patterns of reduction in coral recruitment following disturbance events.

1 3.2. Coral recruitment on settlement plates after the 2005 bleaching event

2

3 The number of recent, live recruits observed on settlement plates between
 4 2007 and 2008 confirmed findings from our RPF modelling. Limited coral
 5 recruitment occurred after 6 and 12 months (Figure 4) with a total of 12 (n = 6 sites)
 6 and 17 recruits (n = 5 sites) observed respectively on all plates at all 6 sites. Buccoo
 7 had the most recruits after 12 months, with 6 recruits being observed on the 18 plates,
 8 all other sites had ≤ 3 recruits on plates after 12 months. Recruits showed a preference
 9 for vertical tiles (n = 8 and 13) after 6 and 12 months respectively, with cryptic (n = 0
 10 and 4) and exposed (n = 4 and 0) tiles showing limited recruitment. Sisters was the
 11 only site where recruits had a preference for exposed tiles (n = 4) after 6 months.

12

13 4. Discussion

14

15 Our growth modelling and settlement plate experiment indicate that coral
 16 recruitment declined significantly in years following hurricanes, tropical storms and
 17 coral bleaching events. Findings from the settlement plates suggest that recovery can
 18 be slow; in this case more than 2 year after the bleaching event Tobago's coral
 19 recruitment was still limited in terms of numbers and biodiversity. The main
 20 framework builder on Tobago's reefs at the time of this study was *M. faveolata*
 21 (Bouchon et al 2008b), however the live coral cover of this species has fallen
 22 dramatically following the 2005 bleaching event and a subsequent disease outbreak of
 23 yellow band disease is impacting the remaining population (O'Farrel and Day 2005;
 24 Bouchon et al. 2008a; Mallela and Parkinson 2008). In this study, we did not observe
 25 recruitment of *M. faveolata* following the multiple disturbance effects of Hurricane

1 Ivan (2004) and the 2005 – 2006 bleaching event. Limited numbers of juvenile *D.*
 2 *strigosa* and *C. natans* were observed to have successfully recruited post-bleaching.
 3 These findings could have implications for the future health of Tobago's reefs since
 4 the continued occurrence of a diverse range of recruits and juvenile corals is essential
 5 in ensuring healthy, resilient, framework building coral reefs (Smith et al. 2005).

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

16 In Belize, in 1998 coral populations simultaneously experienced a severe coral
 17 bleaching event and Hurricane Mitch. A study of coral recruits (Mumby 1999) found
 18 that whilst bleaching alone had no effect on recruitment density or community
 19 structure, the combined effects resulted in a 20% reduction of pre-disturbance levels.
 20 In Belize only 1% of recruits showed even partial mortality during the 1998 bleaching
 21 event. In contrast 66 % of Tobago's coral colonies suffered from bleaching, with an
 22 estimated 73 % of *C. natans* and *Diploria* spp. dying (Bouchon et al. 2008a). In our
 23 study *Diploria* spp. dominated the limited number of recruits from 2004-2006, with *C.*
 24 *natans* also recruiting in 2006, indicating low levels of recovery for these framework
 25 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 $188 \text{ m}^{-2} \text{ y}^{-1}$, this is higher than those observed in this study where coral settlement on vertical plates at Buccoo equated to $103 (\pm \text{SD } 81) \text{ m}^{-2} \text{ y}^{-1}$. These observations suggest that 12 to 18 months after the bleaching event coral recruitment on Tobago's reefs was still limited when compared to recruitment levels in the early 1990's 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 lose their ability to adapt and regenerate (Adger et al. 2005; Crabbe et al 2009). 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 and 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.

Acknowledgements

JM acknowledges the following for funding: the University of the West Indies (UWI, Trinidad and Tobago), The Buccoo Reef Trust and The GEF funded Integrating Watershed and Coastal Area Management (IWCAM) Tobago Program, Government Research Fund of Trinidad and Tobago, Star-Oddi for sponsoring data loggers Ajoupa Pottery for making settlement plates, and numerous dive buddies and volunteers: Marianna Rampaul, Akilah Stewart, Ryan Manette, Michelle Cazaboum, Coral Cay Conservation & UWI volunteers. MJCC thanks the Earthwatch Institute for funding.

References

- 1 Abrego, D., Ulstrup, K.E., Willis, B.L., van Oppen, M.J.H. 2008. Species-specific
2 interactions between algal endosymbionts and coral hosts define their
3 bleaching response to heat and light stress. *Proceedings of the Royal Society B*
4 275, 2273-2282.
- 5 Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R., Rockstrom, J. 2005. Social-
6 ecological resilience to coastal disasters. *Science* 309, 1036-1039
- 7 Bardsley, W.G. 2009. SIMFIT Manual version 6.0.23. Manchester University.
8 <http://www.simfit.man.ac.uk> pp.67-69.
- 9 Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J., P. 2008. *Climate Change and*
10 *Water*. Technical Paper of the Intergovernmental Panel on Climate Change,
11 IPCC Secretariat, Geneva: pp 210
- 12 Bouchon, C., Portillo, P., Bouchon-Navaro, Y., Max, L., Hoetjes, P., Braithwaite, A.,
13 Roach, R., Oxenford, H., O'Farrel, S., Day, O. 2008a. Status of the coral reefs
14 of the Lesser Antilles after the 2005 bleaching event. In: Wilkinson C, Souter
15 D (eds) *Status of Caribbean coral reefs after bleaching and hurricanes in 2005*.
16 Global Coral Reef Monitoring Network, and Reef and Rainforest Research
17 Centre, Townsville, pp152
- 18 Bouchon, C., Portillo, P., Bouchon-Navaro, Y., Louis, M., Hoetjes, P., De Meyer, K.,
19 Macrae, D., Armstrong, H., Datadin, V., Harding, S., Mallela, J., Parkinson,
20 R., van Bochove, J., Wynne, S., Lirman, D., Herlan, J., Baker, A., Collado, L.,
21 Nimrod, S., Mitchell, J., Morrall, C., Isaac, C. 2008b. Chapter 19. Status of
22 coral reefs of the Lesser Antilles: The French west indies, The Netherlands
23 Antilles, Anguilla, Grenada, Trinidad & Tobago. In: Wilkinson C (ed) *Status*
24 *of coral reefs of the world 2008*. Global Coral Reef Monitoring and Reef and
25 Rainforest Research centre, Townsville, Australia, p265-279

- 1 Burke, L., Greenhalgh, S., Prager, D., Cooper, E. 2008. Coastal capital - economic
2 valuation of coral reefs in Tobago and St Lucia. World Resources Institute pp
3 76
- 4 Carricart-Ganivet, J. P. , Beltran-Torres, A. U. , Merino, M., Ruiz-Zarate, M. A. 2000.
5 Skeletal extension, density and calcification rate of the reef building coral
6 *Montastrea Annularis* (Ellis and Solander) in the Mexican Caribbean. Bulletin
7 of Marine Science 66, 215-224
- 8 Coles, S.L., Brown, E.K. 2007. Twenty-five years of change in coral coverage on a
9 hurricane impacted reef in Hawai'i: the importance of recruitment. Coral Reefs
10 26, 705-717.
- 11 Connell, J.H. 1997. Disturbance and recovery of coral assemblages. Coral Reefs 16,
12 s101-s113
- 13 Connell, J.H., Hughes, T., P., Wallace CC 1997. A 30 year study of coral abundance,
14 recruitment, and disturbance at several scales in space and time. Ecological
15 Monographs 67, 461-488
- 16 Cortes, J.N., Risk, M.J. 1985. A reef under siltation stress: Cahuita, Costa Rica.
17 Bulletin of Marine Science 36(2):339-356
- 18 Crabbe, M.J.C. 2009. Scleractinian coral population size structures and growth rates
19 indicate coral resilience on the fringing reefs of North Jamaica. Marine
20 Environmental Research. 67, 189-198.
- 21 Crabbe, M.J.C. Smith, D.J. 2005. Sediment impacts on growth rates of *Acropora* and
22 *Porites* corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24,
23 437-441.

- 1 Crabbe, M.J.C., Mendes, J.M., Warner, G.F. 2002. Lack of recruitment of non-
2 branching corals in Discovery Bay is linked to severe storms. *Bulletin of*
3 *Marine Science* 70, 939-945.
- 4 Crabbe, M.J.C., Walker, E.L.L., Stephenson, D.B. 2008a. The impact of weather and
5 climate extremes on coral growth. In : H. Diaz & R. Murnane (Eds.) *Climate*
6 *Extremes and Society*. Pp. 165-188, Cambridge University Press, Cambridge,
7 UK.
- 8 Crabbe, M.J.C., Martinez, E., Garcia, C., Chub, J., Castro, L., Guy, J. 2008b. Growth
9 modelling indicates hurricanes and severe storms are linked to low coral
10 recruitment in the Caribbean. *Marine Environmental Research* 65, 364-368.
- 11 Crabbe, M.J.C., Martinez, E., Garcia, C., Chub, J., Castro, L., Guy, J., 2009.
12 Identifying management needs for coral reef ecosystems. *Sustainability:*
13 *Science, Practice & Policy*. In the Press.
14 <http://ejournal.nbii.org/archives/vol5iss1/communityessay.mjcrabbe.html>
- 15 Dodge R, E., Vaisnys JR 1975. Hermatypic coral growth banding as environmental
16 recorder. *Nature* 258, 706-708
- 17 Douglas, A. E. 2003. Coral bleaching - how and why? *Marine Pollution Bulletin*
18 46:385-392
- 19 Elsner, J.B., Jagger, T.H., Tsonis, A.A., 2006a. Estimated return periods for Hurricane
20 Katrina. *Geophysical Research Letters* 33, doi:10.1029/2006GL025452.
- 21 Elsner, J.B., Murnane, R.J., Jagger, T.H., 2006b. Forecasting U.S. hurricanes 6
22 months in advance. *Geophysical Research Letters* 33,
23 doi:10.1029/2006GL025693.

- 1 Gilmour, J.P. 1999. Experimental investigation into the effects of suspended sediment
2 on fertilisation, larval survival and settlement in scleractinian coral. *Marine*
3 *Biology* 135, 451-462
- 4 Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the
5 world's coral reefs. *Marine and Freshwater Research* 50, 839-866
- 6 Hubbard, D.K., Scaturro, D. 1985. Growth rates of seven species of scleractinian
7 corals from Cane Bay and Salt River, St Croix, USVI. *Bulletin of Marine*
8 *Science* 36, 325-338
- 9 Hughes, T.P., Jackson, J.B.C. 1980. Do corals lie about their age? Some demographic
10 consequences of partial mortality, fission, and fusion. *Science* 209, 713-715
11
- 12 Hughes, T.P., Tanner, J.E. 2000. Recruitment failure, life histories, and long-term
13 decline of Caribbean corals. *Ecology* 81, 2250-2263
- 14 Huston, M. 1985. Variation in coral growth rates with depth at Discovery Bay,
15 Jamaica. *Coral Reefs* 4, 19-25
- 16 Knowlton, N., Lang, J.C., Rooney, M.C., Clifford, P. 1981. Evidence for delayed
17 mortality in hurricane-damaged Jamaican staghorn corals. *Nature* 294, 251-
18 252
- 19 Laydoo, R.S. 1993. Coral recruitment and transplanation in reef mangement: Buccoo
20 Reef, Tobago. Unpublished MPhil. Thesis. University of the West Indies,
21 Trinidad and Tobago, pp105
- 22 Loya, Y. 1976. Effects of turbidity and sedimentation on the community structure of
23 Puerto Rican Corals. *Bulletin of Marine Science* 26, 450-466

- 1 Mallela, J. 2007. Coral reef encruster communities and carbonate production in
2 cryptic and exposed coral reef habitats along a gradient of terrestrial
3 disturbance. *Coral Reefs* 26, 775-785
- 4 Mallela, J., Perry, C.T. 2007. Calcium carbonate budgets for two coral reefs affected
5 by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs* 26,
6 53-68
- 7 Mallela, J., Parkinson, R. 2008. Coral disease succession in Tobago: from yellow
8 band to black band disease. *Coral Reefs* 27, 787
- 9 Mallela, J., Harrod, C. 2008. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ reveal significant differences in the
10 coastal foodwebs of the seas surrounding the islands of Trinidad and Tobago.
11 *Marine Ecology Progress Series* 368, 41-51
- 12 Meesters, E.H., Hilterman, M., Kardinaal, E., de Vries, M., Bak, R.P.M. 2001. Colony
13 size-frequency distributions of scleractinian coral populations: spatial and
14 interspecific variation. *Mar Ecol Prog Ser* 209, 43-54
- 15 Mumby, P.J. 1999. Bleaching and hurricane disturbances to populations of coral
16 recruits in Belize. *Marine Ecology Progress Series* 190, 27-35
- 17 O'Farrel, S., Day, O. 2005. Report on the 2005 Mass coral bleaching event in Tobago.
18 Part 1. Results from phase 1 survey. Buccoo Reef Trust and Coral Cay
19 Conservation pp 42. http://www.buccooreef.org/Coral_Bleaching_Report_1.pdf
- 20 Smith, L.D., Devlin, M., Haynes, D., Gilmour, J.P. 2005. A demographic approach to
21 monitoring the health of coral reefs. *Marine Pollution Bulletin* 51:399-407
- 22 Szmant, A.M. 1986. Reproductive ecology of Caribbean reef corals. *Coral Reefs* 5,
23 43-53

- 1 Vermeij, M.J.A., Fogarty, N.D., Miller, M.W. 2006. Pelagic conditions affect larval
2 behavior, survival, and settlement patterns in the Caribbean coral *Montastraea*
3 *faveolata*. Marine Ecology-Progress Series 310, 119-128
4
5

ACCEPTED MANUSCRIPT

1 **Legends to Figures**

2

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

6

7 Figure 2. The estimated year of recruitment for all coral colonies in this study 1980-
8 2006 (solid black line), solid arrows indicate when hurricanes, tropical storms (TS)
9 and bleaching events occurred. Dashed arrows indicate events which may have
10 impacted Tobago's reefs but were not cited in records. The histogram underneath
11 gives the estimated year of recruitment for dominant coral species: *Colpophyllia*
12 *natans* (green), *Diploria labyrinthiformis* (dark grey), *Diploria strigosa* (yellow),
13 *Montastrea cavernosa* (light grey), *Porites astreoides* (white), *Siderastrea siderea*
14 (black).

15

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

19

20 Figure 4. Coral recruitment on settlement plates after the 2005 bleaching event. Box
21 whisker plots detailing coral recruitment after 6 and 12 months on settlement plates at
22 10m. Reef sites: Kariwak (K), Buccoo (B), Mt Irvine (M), Culloden (C), Little
23 Englishman's Bay (L), Sisters (S). Plates positioned in 3 orientations horizontal
24 exposed (e), horizontal cryptic (c), vertical (v). Note 12 month tiles at Sisters were
25 lost.

1 Fig.1

2

1 Fig.2

1 Fig.3

2

1 Fig.4