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Spatial and temporal patterns of coral black band disease in relation to a major sewage outfall

Ross Jones[1,*], Rodney Johnson[2], Tim Noyes[2], Rachel Parsons[2]

[1]Australian Institute of Marine Science, The UWA Oceans Institute (M096), 35 Stirling Highway, Crawley, Western Australia 6009, Australia

[2]Bermuda Institute of Ocean Sciences (BIOS), 17 Biological Lane, St Georges, Bermuda GE01

ABSTRACT: Spatial and temporal patterns of coral black band disease (BBD) prevalence were examined during the summers of 2004 to 2008 at 10 reef sites located along a sewage gradient on either side of a major marine outfall on Bermuda's south shore. The gradient was identified by current meter and drogue deployments and confirmed by a water quality monitoring using fecal indicator bacteria (gastrointestinal enterococci) as a sewage marker. BBD prevalence was also examined at 22 locations across the Bermuda platform in different physiographic reef zones, identified by reef survey techniques and analysis of community composition. BBD prevalence was generally low and was recorded in *Diploria strigosa* > *Montastraea franksi* > *M. cavernosa* = *D. labyrinthiformis* > *Porites astreoides* and the hydrocoral *Millepora alcicornis*. Most occurrences were in *D. strigosa*, and BBD prevalence was highest on the outer rim reef (range: 0.3 to 1.9%), followed by the outer lagoonal patch reefs (range: 0.05 to 0.8%) and the deeper terrace reefs (range: 0.1 to 0.2%). BBD prevalence levels decreased over the study period, and BBD was only rarely observed in *D. labyrinthiformis*, which appears to be immune to infection in Bermuda. The BBD prevalence in *D. strigosa* was lower on reefs regularly exposed to sewage than on the near pristine outer rim reef sites, which experience the exceptional water quality characteristics of the oligotrophic North Atlantic gyre.

KEY WORDS: Coral · Black band disease · Sewage · Bermuda

INTRODUCTION

Disease is an important factor affecting the composition, structure and dynamics of coral communities (Edmunds 1991, Hughes 1994, Hayes & Goreau 1998, Goreau et al. 1998, Aronson & Precht 2001, Weil et al. 2002). Nevertheless, the pathology, etiology and epizootiology of most coral diseases remain poorly understood (Richardson 1998, Weil et al. 2002). In particular, the link between disease prevalence and anthropogenic pollution is one of the least understood areas (Richardson 1998, Kuta & Richardson 2002). However, it has been suggested that for coral black band disease (BBD), there is an obvious spatial and temporal relationship with pollution, that it is common in polluted shallow water, that the largest impacts are in areas near sewage outfalls and that it has spread in time and space as human developments spread along coastlines (Goreau et al. 1998).

It was on Bermuda's reefs that BBD was first described by Garrett & Ducklow (1975). This was the first coral disease published in the scientific literature (preceding Antonius 1976, which is always incorrectly cited as having been published in 1973). BBD is a highly conspicuous disease, characterized by a dark, cyanobacterial-dominated, sulfide-rich band that migrates over the surface of corals at rates of several mm d^{-1}, lysing the coral tissue (Rützler & Santavy 1983). The disease is thought to be caused by a consortium of microorganisms and may not have a primary pathogen (Richardson 1998, 2004, Frias-Lopez et al. 2004). BBD is recognized as one of the

*Email: r.jones@aims.gov.au

most widespread diseases in the Caribbean and adjacent waters (Antonius 1981, Weil 2004), primarily infecting massive frameworkbuilding scleractinian corals, including *Diploria* spp., *Montastraea* spp., *Colpophyllia natans* and *Siderastrea siderea* (Antonius 1981, Edmunds 1991, Sutherland et al. 2004). The disease is now recognized as having a global distribution (Sutherland et al. 2004).

A number of field studies have suggested a link between sewage pollution and BBD outbreaks. Taylor (1983) reported an association between BBD prevalence and sewage pollution or poor water quality, but the study does not show any data, and reference is made to other still unpublished work by the same author suggesting the association. Antonius (1985) purports to show a link between disease frequency and sewage pollution, but again, the evidence is based upon a perceptible increase in BBD frequency near a sewage outfall; no data are shown. Kaczmarsky et al. (2005) recorded a significantly higher prevalence of BBD and White Plague type II in corals at a single location compared to a single control site 2.5 km away. The site where the disease prevalence was higher was occasionally exposed to un-treated sewage (during emergency sewage bypass events). Kuta & Richardson (2002) found a positive relationship between elevated nitrite and BBD prevalence in Florida but did not find an overall positive correlation with the more readily assimilable nutrient species. Overall, the results are difficult to interpret, and any relationship between poor water quality and BBD remains obscure (Richardson 2004).

Located in the mid-Atlantic ~1500 km north of the Caribbean and 1000 km east-southeast of the US, Bermuda is made up of a crescent-shaped chain of ~150 islands (land area of 53 km^2) restricted to the SE corner of an atoll-like elliptical reef tract (Morris et al. 1977). Bermuda is highly geographically isolated and generally recognized as containing the most northerly reefs of the Atlantic (Spalding et al. 2001). With just over 30 hard coral species, the reefs are depauperate compared to the >65 species (from >20 genera) reported in the Caribbean (Stehli & Wells 1971, Wells 1973, Sterrer 1986, Logan 1988).

Bermuda is densely populated, and surveys of chemical contamination of sediments have identified a number of pollution 'hotspots' (Jones 2011), including a reef beside a marine landfill (seafill), which was proposed as the most contaminated reef in the world (Jones 2010). Recent surveys of sewage pollution have also shown a number of areas with high fecal indicator bacteria (gastrointestinal enterococci) in seawater and areas where sediments contain the human specific bacterial biomarker *Bacteroides* and elevated concentrations of the fecal biomarker coprostanol (5β-cholestan-3-β-ol; Jones et al. 2011).

The sewage (and chemical) pollution 'hotspots' are invariably located inshore, in enclosed bays, harbors, marinas and where there are houses or light industry located close to the shoreline (Jones 2011, Jones et al. 2011). The patch reefs of the Bermuda lagoon and offshore, outer reef systems are relatively contaminant-free (Jones 2011), probably due to the absence of any river systems that can transport anthropogenic material offshore. There is, however, a large sewage outfall on Bermuda's south shore which continuously discharges ~2.5×10^6 to 5×10^6 l d^{-1} of virtually untreated sewage. The outfall (Seabright Point) was established in 1992 and serves the capital city of Hamilton and surrounding areas, a local hospital and cruise ships docked at Hamilton during the summer months. Prior to discharge, the sewage is only subject to preliminary treatment, which involves maceration (i.e. grinding up of soft solids), screening (i.e. straining for solid trash) and removal of sand and larger inorganic particles (see Tchobanoglous & Kreith 2002). The sewage is released over a ~100 m long area through a series of ten 1.5 m high riser jets (which discharge alternately in opposite directions) and through a terminal (end) diffuser, which is mounted ~1 m above the seabed. The end diffuser is ~630 m from the shore and close to the deeper (15 to 18 m) main terrace reef system (see Logan 1988 for terminologies). Sewage disposal options and practices in Bermuda are discussed further by Jones et al. (2011).

Bermuda's reefs are considered to be under significant environmental pressure (see Burke & Maidens 2004), because of the high population density and because reefs with low species diversity have a low capacity to absorb a disturbance due to low functional redundancy, i.e. they have a low resilience (Folke et al. 2004). Coral growth is also limited in high-latitude reefs by lower water temperatures and aragonite saturation state (Kleypas et al. 2001), and highly isolated reefs are also likely to recover more slowly from disturbances than central, more interconnected populations (Hughes et al. 2003). In vulnerable reef systems, the effect of anthropogenic agents (such as sewage pollution) on disturbance agents like BBD is of particular interest, since pollution can be theoretically prevented, unlike the disturbances related to climate change.

We conducted hydrological studies around the sewage outfall on Bermuda's south shore to guide selection of survey sites along a putative sewage contamination gradient. We confirmed the gradient by testing for fecal indicator bacteria (enterococci) and then, in annual surveys conducted over a 5 yr period, examined BBD prevalence on reefs along the gradient. To provide a wider context for these studies and to examine the significance of BBD as a factor structuring the reef communities of Bermuda, we also examined the composition, coral distribution patterns and BBD prevalence in different physiographic reef zones across the Bermuda platform. The results are discussed in terms of the links between BBD and sewage pollution but also in terms of the overall risk posed by BBD to these highly isolated, high latitude reefs of Bermuda.

MATERIALS AND METHODS

Spatial patterns of coral cover and disease prevalence

Videographic surveys of the coverage of major benthic groups were conducted at multiple locations across the Bermuda platform encompassing different physiographic reef zones (using the terminology of Logan 1988), including the platform margin reefs (i.e. rim reefs, 8 to 10 m depth; A, A2, B and B2 in Fig. 1A), offshore lagoonal patch reefs (3 to 5 m depth; C, C2, D and D2 in Fig. 1A,B), nearshore patch reefs (3 to 5 m depth; E, E2, F and F2 in Fig. 1A,B), inshore patch reefs (3 to 5 m depth; G and G2 in Fig. 1A,B), inshore fringing reefs (3 to 5 m depth; H and H2 in Fig. 1A,B) and main terrace reefs (15 to 18 m depth; I, I2, J, J2, K and K2 in Fig. 1A,B). All of the monitoring sites were established in 2004, except sites H and H2, which were established in 2005. Video surveys were conducted from mid-July to mid-September each year.

At each 'location' within a physiographic reef zone, 2 study sites were chosen (i.e. A, A2 or B, B2, etc.) separated by a distance of at least 300 m. At each 'site', generally an individual reef, five 30 m parallel permanent transects were established, separated from each other by a distance of at least 3 to 5 m. The start, middle and end of the transect lines were marked with a 30 to 40 cm section of 15 mm galvanized reinforcing rod hammered into the reef.

During surveys, the reef was recorded using a digital video recorder mounted in an underwater video housing. Filming followed the contours of the reef, perpendicular to and 0.5 m from the reef, and was conducted between 09:00 and 15:30 h for optimum lighting conditions. In the laboratory, 50 non-overlapping still images were captured from each transect line video using video editing software. The software program CPCe (Coral Point Count, NCRI) was used for image processing (Kohler & Gill 2006) using 10 points randomly distributed across each of

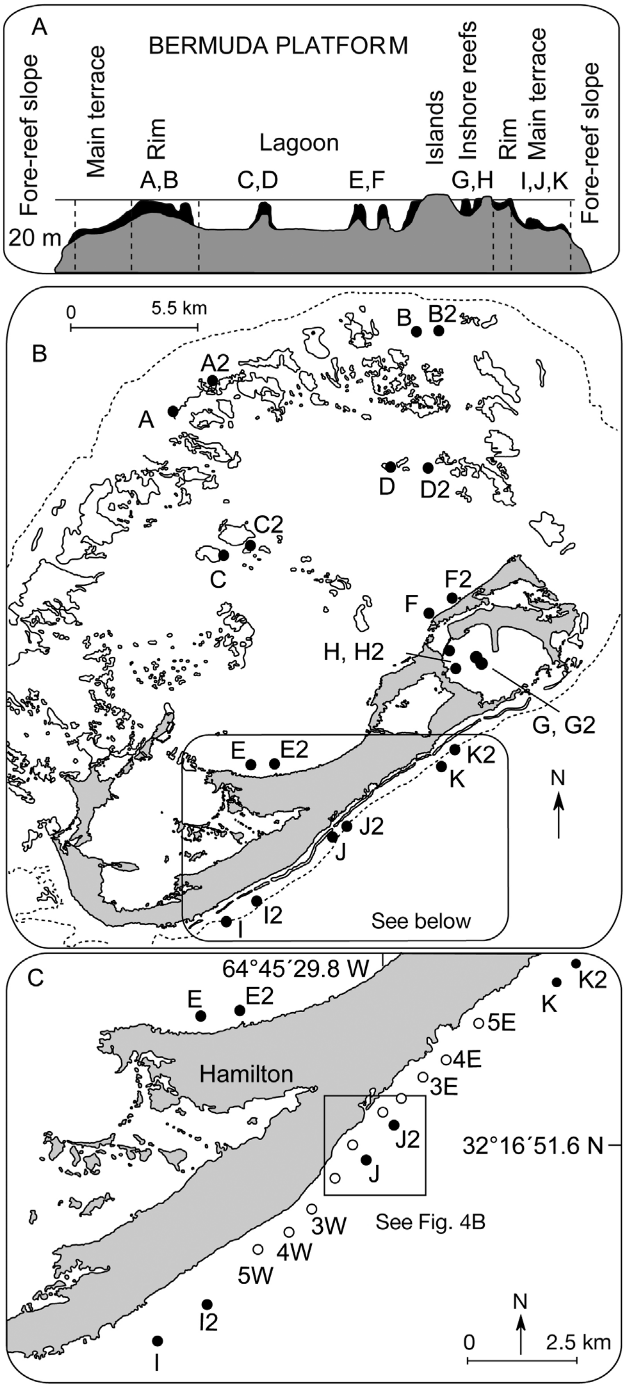

Fig. 1. (A,B) Long-term video monitoring sites and disease monitoring locations (●, A to K). (C) 10 coral disease survey sites along the south shore of Bermuda (O, W & E), centered around the Seabright Point sewage outfall

the 50 images from a given transect, and the coral species or substrate lying under these points was identified. For CPCe analysis, 12 categories specific to Bermuda were used including 9 'living' categories (i.e. 'hard corals', 'gorgonians', etc.) and 3 'non-living' categories (sand, rock or rubble, etc.). Organisms were identified to the highest level of taxonomic certainty.

Hydrological studies

The flow characteristics around the Seabright Point sewage outfall were investigated to understand the dispersion of the sewage plume and guide placement of the ecological survey and water quality survey sites along a sewage gradient. Current speed and direction was measured with an Aanderaa, RCM 9 MkII acoustic doppler current meter (Aanderaa Nesttunbrekken 97, 5221 Nesttun) deployed 30 m SE of the outfall at mid-water (i.e. ~10 m depth, to avoid noise from wave pumping) using a mooring weight and subsurface buoy. The current meter was set to record at 10 min intervals the speed and direction, which were calculated as vector averages for the sampling period, and the pressure and temperature readings were taken every 10 min. Wind speed and direction data for these deployments were provided by the Bermuda Weather Service as recorded at the Bermuda International Airport.

Currents in the vicinity of the outfall have been examined by drogue studies in 1973 by the Bermuda Government, then the Ministry of Works and Agriculture, as part of an investigation of potential offshore outfall sites. In the absence of any major modification to the shoreline in the interim period that may affect flow regimes, the results of the drogue studies are considered still applicable, and the results of the study have been included to supplement the eulerian studies described above. In the study, drogues were deployed at 1, 3 and 9 m deep and allowed to drift, and their positions were fixed after 1 h and 2 h. Studies were conducted over 9 d under different combinations of tide and wind direction.

To examine water quality associated with the sewage outfall, seawater samples were collected along the putative sewage gradient (Sites K2, 5E, 1E, J2, J, 1W, 5W and I2 in Fig. 1B). Water samples were collected in June 2010 (on a flooding tide) and stored chilled until analysis at the Bermuda Government Department of Health within 6 h of collection. All of the samples were analyzed for fecal indicator bacteria (enterococci) using culture-dependent membrane filtration techniques (EPA 2000, WHO 2003), and the data were expressed as the number of colony forming units (CFUs) per 100 ml.

BBD disease surveys

During the video surveys, assessments were made of the prevalence of BBD in hard coral species and the hydrocoral *Millepora alcicornis*. All assessments were made along a 1 m band on either side of the transect tapes used in the video monitoring. To examine the relationship between BBD prevalence and proximity to the Seabright Point sewage outfall, assessments were also made on five 30 m parallel transects at 5 nearshore reefs (8 to 10 m depth) located between 0.5 and 3.3 km east and west of the sewage outfall, along the primary axis of sewage flow identified by hydrological studies (Sites E1 to E5 and W1 to W5 in Fig. 1B,C). Disease surveys were conducted at these sites from mid-July to mid-September each year.

Statistical analyses

Multivariate analysis techniques were used to examine the community structure of the reefs and spatial distributions of the study species. Because 2005 was the first year in which all permanent monitoring sites were established, data from 2005 were used for the analysis. From the abundance data, hierarchical clustering analysis was used to produce dendrograms (tree diagrams) in which a series of nested groupings of sites were constructed, with biologically similar samples clustering close together and dissimilar samples spaced farther apart. Multidimensional scaling (MDS) analysis (Shepard 1962), based on Bray-Curtis similarities from square root transformed data, was then used to produce a map of the study sites that reflects their biological similarity (in terms of species, benthic class or species group) rather than cluster location.

To test for the relationship between BBD prevalence and the sewage outfall, the prevalence data were analyzed by fitting a generalized linear model (GLM) using a Poisson distribution with a log link. The model was fitted with direction, distance and their interaction, using an offset of the total number of colonies. The Poisson distribution was used because this is the most appropriate for data with small counts, and the offset takes into account the proportion of diseased coral, not just the actual count. The prevalence of disease was very small (0 to 6 cases or 0 to 5%) in each transect line, and the transect lines were grouped together at each site to give a total number of cases for each location. Each year of measure was treated as a replicate, and the distance from the outfall was fitted as a factor.

RESULTS

Spatial patterns of coral cover

In total, 15 hard coral species were recorded during the video-monitoring program surveys of 2005. Coral cover was higher on the main terrace reefs (mean ~60% hard coral cover) than the rim reef sites (mean ~25%) and lagoonal patch reefs (mean ~17%; Table 1). The inshore fringing and patch reefs (Locations G and H) had ~5% hard coral cover (Table 1).

The multivariate analysis of the video-survey data shows 3 primary clusters based on 60% similarity patterns (Clusters 1 to 3 in Fig. 2A) and 2 secondary clusters (i.e. Sub-clusters 2A and 2B in Fig. 2A) based on 65% similarity patterns. The stress value associated with the plot was 0.14, indicating a good representation of between-site differences in the 2-dimensional picture. Both sites at each 'location' were always found within the same primary cluster; for example, all outer rim reef sites (i.e. Locations A and B) were located within Cluster 1, and all offshore lagoonal patch reef sites were located in Cluster 2. Similarly, the inshore fringing and patch reefs (G and H) were located in Cluster 2B. The nearshore lagoonal coral-algal patch reefs of Site E formed a separate cluster (Cluster 3 in Fig. 2A).

The *Diploria-Montastraea-Porites* species assemblage constitutes ~97% of the hard coral cover in Cluster 1 (which includes the rim reef and main terrace reef), nearly 90% of Cluster 2A (lagoonal patch reefs) and nearly 70% of Cluster 2B (the inshore patch and fringing reefs) but only ~16% of Cluster 3 (see pie-charts in Fig. 2A, Table 1). Cluster 3 represents turbid near shore patch reefs, which, although they have an average hard coral cover of 22%, are dominated by branching species, such *Madracis mirabilis*, *M. decactis* and the hydrocoral *Millepora alcicornis* (see pie-charts in Fig. 2A, Table 1). In Cluster 1 (which constitutes the bulk of Bermuda's reefs),

Table 1. Cover (mean percentage total cover ± SD) of hard corals (including the hydrocoral *Millepora alcicornis*) and major benthic groups at the 10 video monitoring locations (see Fig. 1A), with each location comprising 2 sites. D-M-P: *Diploria-Montastraea-Porites*

MDS cluster: Location:	Cluster 1 A, B	Cluster 1 I, J, K	Cluster 1 A, B, I, J, K	Cluster 2A C, D, F	Cluster 2B G, H	Cluster 3 E	All sites
% D-M-P assemblage	96.9 ± 2	99.4 ± 0.5	98.4 ± 1.8	88.4 ± 4.6	66 ± 14.1	15.9 ± 1.8	85.9 ± 26
Diploria spp. (%)	72.2 ± 3	73 ± 3.4	72.7 ± 3.1	29.8 ± 18	50.8 ± 9.1	2.1 ± 0.1	50.5 ± 28.6
D. strigosa (%)	41 ± 1.2	54.3 ± 4.1	49 ± 7.5	18.9 ± 17	5.6 ± 4	0.9 ± 0.4	33.6 ± 21.4
D. strig.:*D. lab.* (ratio)	1.42 ± 0.03	3.42 ± 1.04	2.62 ± 1.29	2.20 ± 1.27	0.22 ± 0.13	–	2.39 ± 1.25
% of hard coral cover							
Diploria labyrinthiformis	31.1 ± 2	18.7 ± 3.1	23.6 ± 7	10.9 ± 5.2	45.2 ± 9	1.2 ± 0.5	16.9 ± 10.1
Diploria strigosa	41 ± 1.2	54.3 ± 4.1	49 ± 7.5	18.9 ± 17	5.6 ± 4	0.9 ± 0.4	33.6 ± 21.4
Montastraea cavernosa	2 ± 1.4	5.3 ± 1.9	4 ± 2.4	11.2 ± 10.2	0.5 ± 1	0.1 ± 0.1	6 ± 7
Montastraea franksi	13.7 ± 5.3	16.1 ± 4.6	15.1 ± 4.8	38.5 ± 20.1	2.8 ± 2.1	2.7 ± 0.2	21.5 ± 17.3
Porites astreoides	9.1 ± 5	5 ± 1.8	6.6 ± 3.8	8.8 ± 3.5	12 ± 7.4	11 ± 1.6	7.9 ± 3.7
Madracis decactis	0 ± 0	0.1 ± 0.2	0 ± 0.1	1.5 ± 2.2	8 ± 4.2	5.1 ± 1.2	1.1 ± 2
Madracis mirabilis	0 ± 0	0 ± 0	0 ± 0	1.1 ± 1.9	10.9 ± 4.9	43.6 ± 5.9	5.2 ± 14.1
Millepora alcicornis	2.8 ± 2	0.3 ± 0.4	1.3 ± 1.7	7.4 ± 5.4	2.1 ± 2.2	30.9 ± 2.9	6.6 ± 9.8
Benthic category cover							
Hard corals	25.0 ± 3.5	57.7 ± 6.6	44.6 ± 17.7	17.2 ± 7.5	4.9 ± 1.2	21.7 ± 3.8	32.9 ± 19.1
Gorgonians	8.7 ± 2.2	4.1 ± 2.3	5.9 ± 3.2	3.0 ± 1.8	5.3 ± 3.3	1.4 ± 0.1	4.4 ± 3.1
Zoanthids	0.0 ± 0.0	0.3 ± 0.5	0.2 ± 0.4	0.2 ± 0.3	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.4
Sponges	0.1 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	2.2 ± 1.5	1.3 ± 0.5	3.8 ± 1.7	1.2 ± 1.6
Anemones/Ascidians/ Corallimorphs	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.2	0.3 ± 0.1	0.1 ± 0.0	0.2 ± 0.2
Macroalgae	22.5 ± 13.2	11.5 ± 7.3	15.9 ± 11.0	11.6 ± 4.0	25.1 ± 19.9	33.9 ± 0.8	16.4 ± 10.6
Turf algae	38.5 ± 7.9	24.0 ± 5.9	29.8 ± 9.8	47.1 ± 9.4	50.6 ± 16.9	22.1 ± 0.5	34.7 ± 12.8
Coralline algae	1.2 ± 0.6	0.9 ± 0.3	1.0 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.1	0.6 ± 0.6
Abiotic	4.0 ± 5.7	1.2 ± 0.6	2.3 ± 3.6	18.6 ± 3.7	12.3 ± 1.8	16.3 ± 2.5	9.3 ± 8.8

the 2 *Diploria* species collectively make up 75% of the hard coral cover, and *D. strigosa* makes up 50% of the coral cover (see pie-charts in Fig. 2A). The ratio of *D. strigosa* to *D. labyrinthiformis* varies from 1.42:1 on the rim reef to 3.42:1 on the main terrace reef (Table 1).

The results from the 2005 surveys can be compared to similar studies conducted on the main terrace and rim reef in the 1980s (see Dodge et al. 1982, Logan 1988). Although the exact location of the earlier surveys are unknown, Fig. 3 shows that for the *Diploria* spp, *Montastraea* spp. and *Porites astreoides*, the present day distribution patterns are essentially the same as in the 1980s, both for the main terrace reef (Fig. 3A) and outer rim reef (Fig. 3B) and in terms of the relative coral cover (%) and absolute coral cover (Fig. 3A,B insets, Table 1).

Hydrological studies

Currents at the sewage outfall site were typically <15 cm s^{-1} (~0.3 knots, see Fig. S1A in the supplement at www.int-res.com/articles/suppl/m462p079_supp.pdf) over the 2 deployments, although for short periods, values exceeded 20 cm s^{-1}, with a maximal value of 30 cm s^{-1} (~0.6 knots) during the second deployment. Currents at the outfall flow in predominantly SW–NE directions, flooding to the SW and ebbing to the NE (see Fig. S1B in the supplement). Data on current and wind speed and direction for the 2 deployments are also included in the supplemental material (Fig. S1A–D). Observation of the flows as a scatter plot for the 2 deployments show that the main axis of flow at the outfall site is from the SW (220 to 230°) to the NE (40 to 50°; Fig. 4A). Further, it appears that flows in the NW and SE sector are not common,

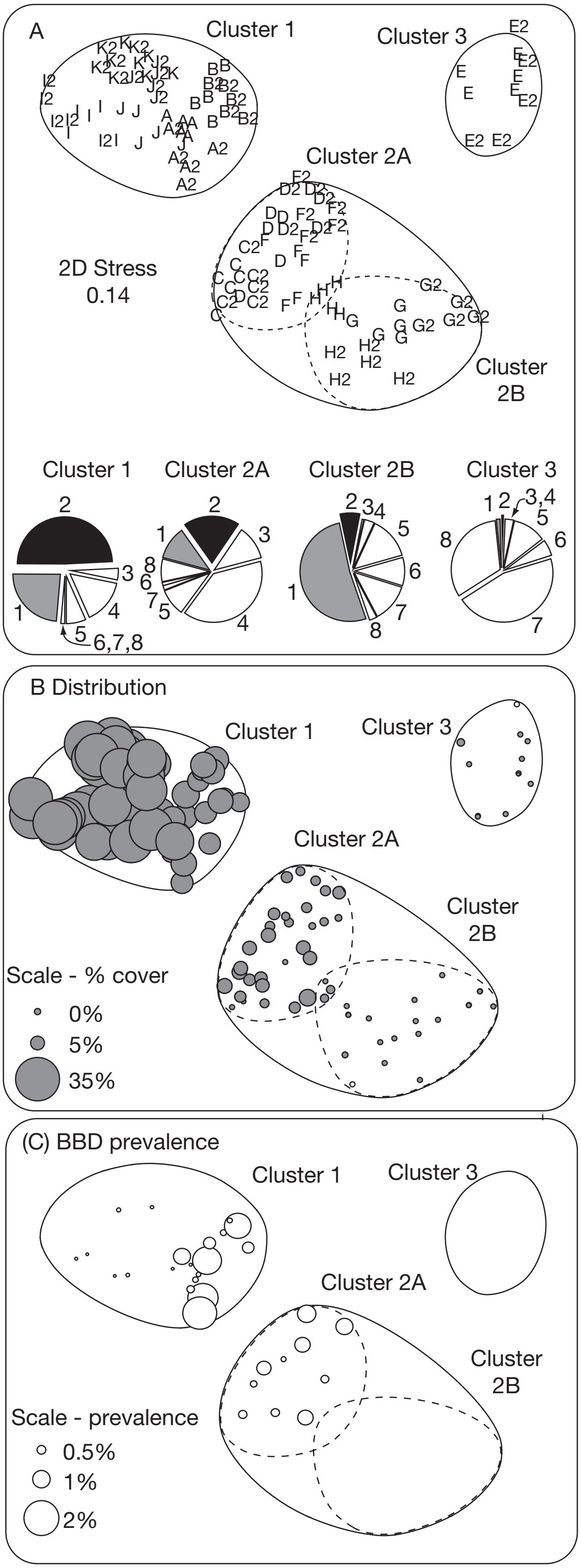

Fig. 2. (A) MDS plots from Bray-Curtis similarities on square-root transformed abundance data (letters refer to individual transect lines at each of the sites shown in Fig. 1A). Clusters 1 to 3 and Sub-clusters 2A and 2B are defined using arbitrarily chosen similarity thresholds of 65% and 60% respectively based on dendrograms from group average clustering of the Bray-Curtis similarities. Pie charts: relative dominance of hard corals based on averages of cover, within each of the clusters of sites identified by the MDS analysis. 1: *Diploria labyrinthiformis* (grey shading), 2: *D. strigosa* (black shading), 3: *Montastraea franksi*, 4: *Porites astreoides*, 5: *Madracis mirabilis*, 6: *Millepora alcicornis*, 7: *Montastraea cavernosa*, 8: *Madracis decactis*, 9: *Stephanocoenia michelinii*, 10: *Oculina* spp., 11: *Siderastrea radians*, 12: *Favia fragum*. (B) MDS plot superimposed with the coverage (%) of *D. strigosa* or (C) BBD prevalence (%) in *D. strigosa*

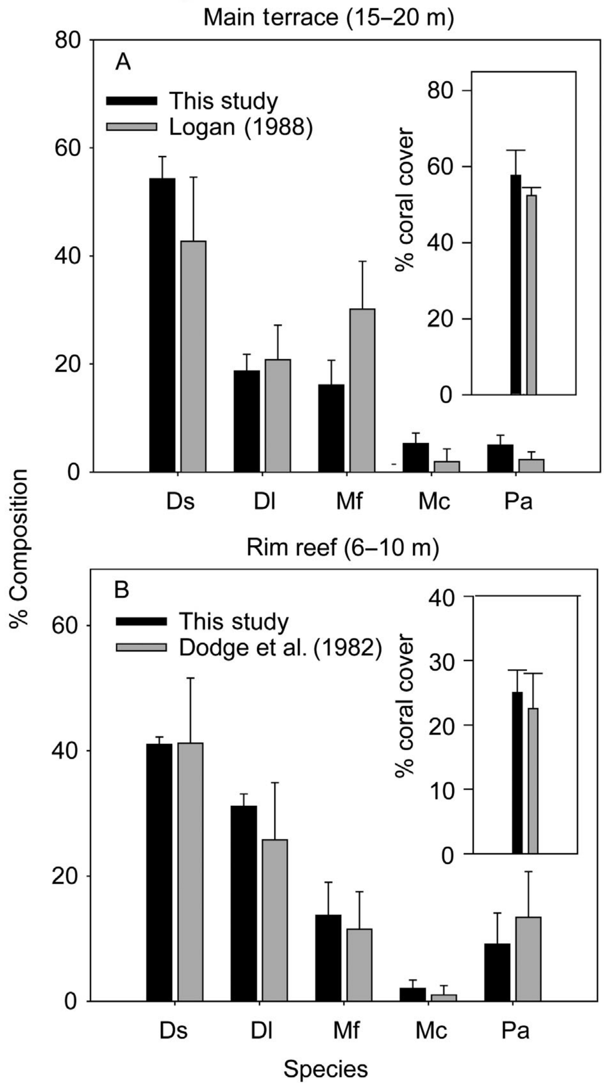

Fig. 3. Relative composition of the (A) main terrace reefs (Sites I, I2, J, J2, K, K2 in Fig. 1A) and (B) outer rim reef (Sites A, A2, B, B2 in Fig. 1A) compared with data from Dodge et al. (1982) and Logan (1988). Insets: absolute hard coral coverage (% cover). Ds: *Diploria strigosa*, Dl: *D. labyrinthiformis*, Mf: *Montastraea franksi*, Mc: *M. cavernosa*, Pa: *Porites astreoides*

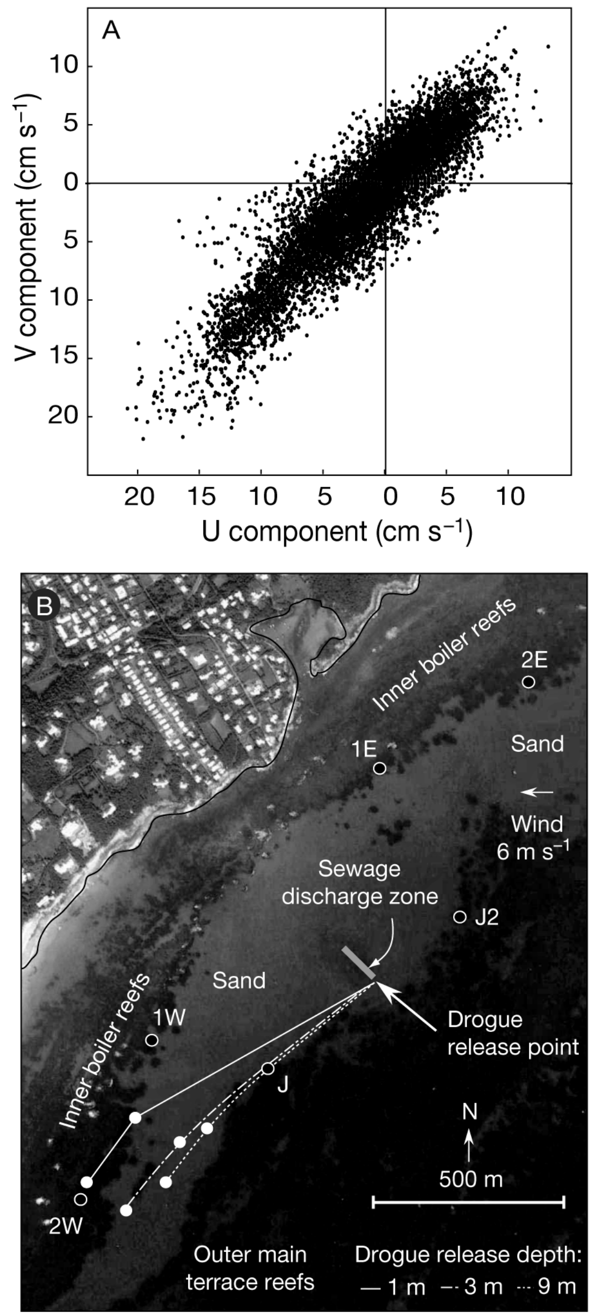

Fig. 4. (A) The distribution of flows at the Seabright Point sewage outfall decomposed into orthogonal velocity components U (west–east direction, with values >0 indicating flow to the east) and V (south–north direction, with values >0 indicating flow to the north), where each point represents a single 10 min vector averaged observation whereby the speed is relative to the distance from the origin (see the supplement at www.int-res.com/articles/suppl/m462p079_supp.pdf for current speed and wind speed and direction). (B) Drogue tracking study, showing the drift of drogues deployed at 1, 3 and 9 m depth on a flooding tide with an onshore wind, relative to the various monitoring sites (see Fig. 1; see supplemental data for additional drogue deployments during different tidal phases and wind directions)

with only 8% and 2% of the total flows respectively, while 27% was to the NE and 63% to the SW sector. Overall, the weakly semi-diurnal characteristic resulted in a biased flow to the SW and a residual flow of ~4.6 cm s^{-1} (~4 km d^{-1}) over the hydrological observation period.

Drogues released on flooding tides moved predominantly in a SW direction irrespective of whether winds were onshore or offshore (Fig. 4B, Fig. S2B,D in the supplement). In one of these studies, conducted with a directly onshore wind, the surface drogue crossed the inner line of boiler reefs and reached the shoreline (Fig. S2B); however, in all other instances, the drogues moved in an approximately longshore direction, maintaining a SW trajectory. On the ebbing tide (i.e. Fig. S2C,E), the flow direction was usually in a NE or E direction, with the surface (1 m depth) drogues being more influenced by wind direction than the deeper drogues (3 and 9 m) during an offshore wind (Fig. S2E).

Based on the hydrological studies, the videographic and disease survey sites were located east and west of the outfall on the closest main terrace reefs within the axis of flow of the sewage plume (see Figs. 1C & 4B). These sites (J and J2) were ~302 m and 333 m NE (58°) and SW (225°) respectively from the terminal diffuser of the outfall, although due to a series of risers before the terminal diffuser, the sewage is released in a ~100 m discharge zone (see Fig. 4B). Ten additional coral disease monitoring sites were located on shallower (8 to 10 m depth) near shore reefs located between ~0.5 km and 3.3 km east and west of the sewage outfall (see Fig. 1C).

Water sampling for fecal indicator bacteria was conducted on a flooding tide, and enterococci counts along the putative gradient ranged from 51 CFUs 100 ml^{-1} at Site J (300 m west of the outfall), to 11 CFUs 100 ml^{-1} at Site I, ~6 km west of the outfall (Fig. 5). Enterococci counts at Site J2 (330 m east of the discharge zone) were 40 CFUs 100 ml^{-1}, but all other sites east of the outfall were below the detection limits (Fig. 5). In additional water sampling immediately around the terminal diffuser in June 2008, values of 2300 and 1300 CFUs 100 ml^{-1} were recorded.

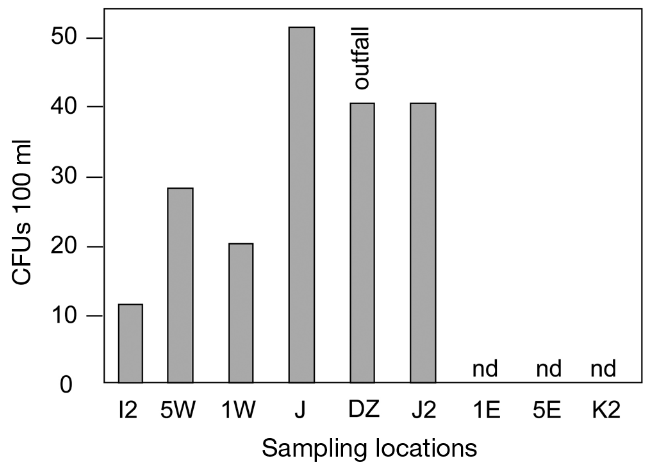

Fig. 5. Fecal indicator bacteria (gastrointestinal enterococci) counts as colony forming units (CFUs) per 100 ml at 9 locations (see Fig. 1B,C) situated from 0.3 to 6 km east and west of the sewage outfall. DZ: samples collected close to the sewage outfall in the Discharge Zone (see Fig. 1C); nd: not detected

Spatial patterns of BBD prevalence

Between 2004 and 2008, a total of 355 incidences of BBD were observed in ~160 000 corals surveyed. BBD was most prevalent in *Diploria strigosa* > *Montastraea franksi* > *M. cavernosa* = *D. labyrinthiformis* > *Porites astreoides* and the hydrocoral *Millepora alcicornis* (Table 2). Overwhelmingly, BBD was most prevalent in the symmetrical brain coral *D. strigosa* (316 incidences), and because it is the most abundant coral in Bermuda, with a wide distribution across the platform (Table 1, Fig. 2B), spatial patterns of BBD prevalence and proximity to the sewage outfall were examined mostly in this species.

BBD was not recorded on any *Diploria strigosa* colonies on the nearshore patch reef sites E and E2, where there was a low abundance of *D. strigosa* (Table 1) and where typically <10 colonies were encountered each year at each site. BBD was also not recorded at Sites G, G2, H and H2, where there was also a low abundance of *D. strigosa* (Table 1) and typically ~30 colonies were examined each year at each

Table 2. Black band disease (BBD) prevalence in 5 coral species in Bermuda from 2004 to 2008. n: number of recorded BBD infections; total: total number of coral colonies examined

Year	*Diploria strigosa*			*Diploria labyrinthiformis*			*Montastraea cavernosa*			*Montastraea franksi*			*Porites astreoides*		
	n	Total	%	n	Total	%	n	Total	%	n	Total	%	n	Total	%
2004	107	11 765	0.91	1	5460	0.02	0	1135	0.00	10	1689	0.59	0	10 612	0.00
2005	92	15 032	0.59	0	6873	0.00	1	1978	0.05	11	2187	0.50	1	13 496	0.01
2006	60	16 998	0.35	1	7858	0.01	2	2124	0.09	5	2434	0.21	0	15 297	0.00
2007	39	17 196	0.23	1	8059	0.01	0	2101	0.00	5	2307	0.22		not surveyed	
2008	22	14 116	0.15	0	6567	0.00	0	1528	0.00	2	1811	0.11			
Totals:	316	75 107	0.44	3	31 812	0.01	3	8865	0.03	33	10 428	0.32	1	39 405	0.00

site. On the outer rim reef (i.e. Sites A, A2, B and B2 in Fig. 1A,B) and on the deeper main terrace reefs (Sites I, I2, J, J2, K and K2 in Fig. 1A,B), *D. strigosa* dominates, and typically between 400 and 1000 colonies of *D. strigosa* were examined at each site each year. On the patch reefs of Cluster 2A (in Fig. 2A, i.e. Locations C, C2, D, D2, F and F2 in Fig. 1A,B), *Diploria* species were less abundant (see Table 1), but between 70 and 200 colonies were examined at each site each year. Between 2004 and 2008, BBD prevalence in *D. strigosa* ranged from 0.0 to 2.8% (Fig. 6 A) on the outer rim reef sites, nearly an order of magnitude higher than on the main terrace, where the BBD prevalence ranged from 0 to 0.8%, Fig. 6A).

In 2003, the maximum average daily seawater temperatures on the outer rim reef (Site A in Fig. 1A,B) was 29.9°C and exceeded 28.5°C on 31 d (Fig. 7A,B). Water temperatures in 2004 and 2005 were higher than those recorded in the summers of 2006, 2007 and 2008, exceeding 28.5°C on 15 d (2004) and 29 d (2005) compared with 3 d (2006), 9 d (2007) and 5 d (2008; Fig. 7B).

Fig. 2 integrates the results from the videographic surveys and analysis of community structure across the platform, the analysis of the hard coral composition and the surveys of BBD prevalence in *Diploria strigosa* (using data from 2005). The plot shows the MDS ordinations of community composition superimposed with bubble plots whereby the size of each bubble reflects either the coverage of *D. strigosa* (Fig. 2B) or BBD prevalence (Fig. 2C). Thus, the highest density of *D. strigosa* is on the deeper (15 to 18 m depth) main terrace sites (I, I2, J. J2, K and K2 in Fig. 1A,B) in Cluster 1, followed by the shallower (8 to 10 m depth) rim reef sites (A, A2, B and B2 in Fig. 1A,B) and then the shallow (~5 m depth) patch reef sites (C, C2, D, D2, F and F2 in Fig. 1A,B; Fig. 2B). BBD prevalence in *D. strigosa* is highest on the outer rim reefs (part of Cluster 1) and lagoonal patch reefs (Cluster 2A), with very low prevalence on the deeper terrace reefs (Fig. 2B), and no recorded BBD incidences in the inshore and near shore patch reefs of Clusters 2B and 3 (Fig. 2C).

Along the contamination gradient on either side of the Seabright Point (i.e. ~500 m and up to 3.3 km

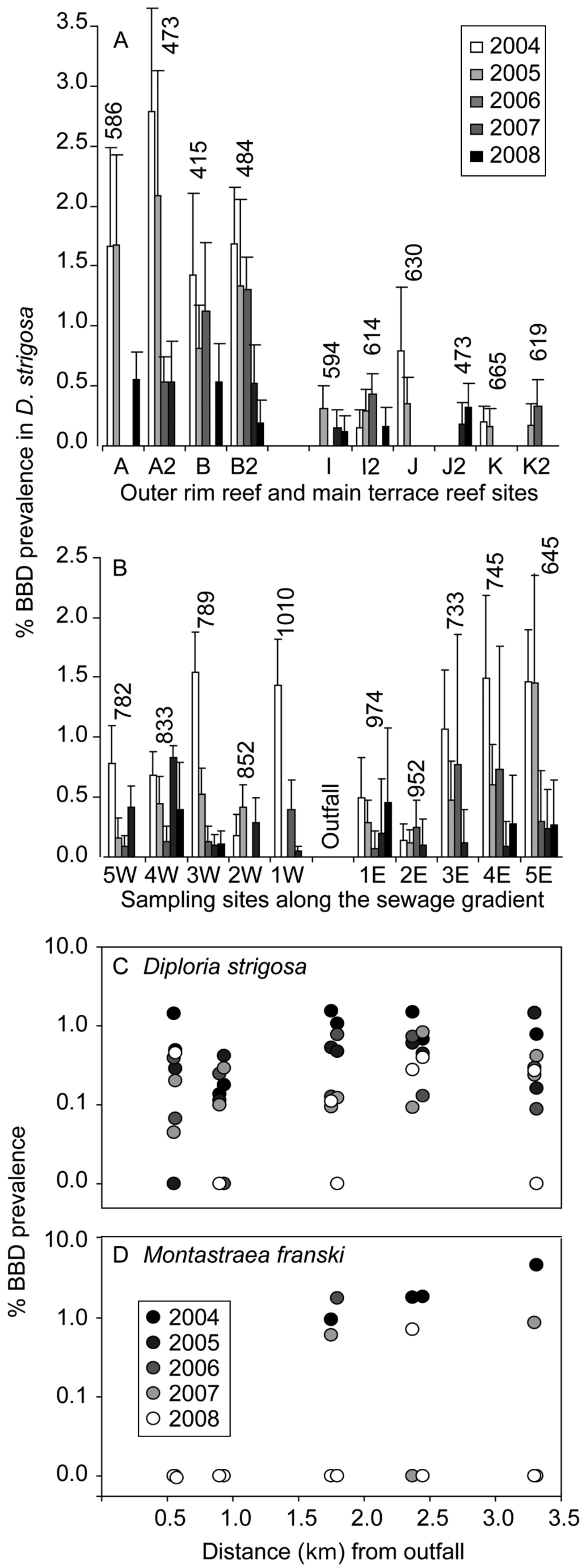

Fig. 6. (A) Black band disease (BBD) prevalence in *Diploria strigosa* in different physiographic reef zones in Bermuda (see Fig. 1A). (B) BBD at 5 nearshore reefs between 0.3 and 3.3 km east and west of the sewage outfall (see Fig. 1B). (C) BBD prevalence plotted against distance (either east or west) from the sewage outfall. All disease surveys were conducted between mid-July and mid-September each year

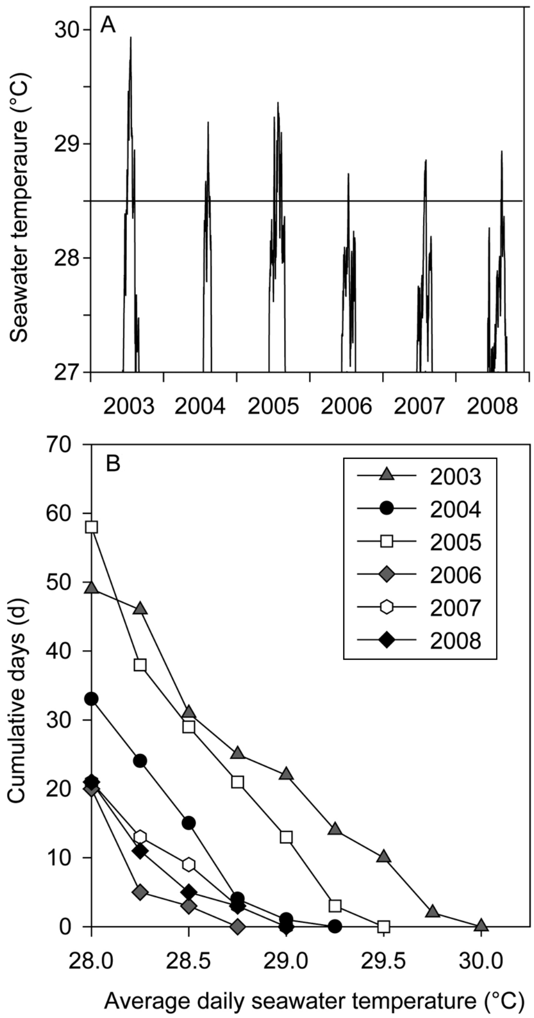

Fig. 7. (A) Average daily seawater temperature (°C) recorded at 8 to 10 m depth on the outer rim reef (Site A2 in Fig. 1A) over the study period. (B) The number of days that average daily seawater temperatures at 8 to 10 m depth on the outer rim reef (Site A2 in Fig. 1A) exceeded a given temperature level (range: 28 to 30°C)

either side of the outfall, see Fig. 1C), BBD prevalence in *Diploria strigosa* was very low throughout the 5 yr study period, ranging from 0% to a maximum of 1.5% (at Sites 3W, 4E and 5E in 2004; Fig. 6B,C). A GLM analysis indicated that the relationship between BBD prevalence in *D. strigosa* and distance from the outfall was not significantly different between the east and west (p-value = 0.16), and thus, the model was fitted without the interaction term. The new model (fitted with only distance) indicates that there is a significant relationship with distance (p-value = 0.0272) and that BBD prevalence increases by a factor of 1.37 with each unit of distance.

There were only 33 incidences of BBD recorded in *Montastraea franksi* over the study period, in contrast to the 316 incidences in *D. strigosa* (Table 1). No BBD infections were recorded at the sites closest to the outfall (Sites 1W, 2W, 1E and 2E) over the 5 yr survey, but some incidences were observed at the sites 1.75, 2.5 and 3.3 km east and west of the outfall in some years (Fig. 6D). The highest BBD prevalence level in *M. franksi* (4.8%) was recorded at Site 5W, 3.2 km west of the outfall in 2004 (Fig. 6D).

DISCUSSION

The relationship between disease prevalence and anthropogenic or pollution effects is one of the least understood areas of coral disease, and the relationship will ultimately be resolved by laboratory experiments, ecological surveys in relation to individual pollution sources and large-scale surveys of prevalence relative to pristine and developed catchments (see Page & Willis 2006). With the caveat that our present study is limited mostly to 1 species (*Diploria strigosa*), overall, there was no obvious relationship between BBD prevalence and proximity to a major sewage outfall. BBD prevalence levels on reefs close to the outfall were consistently lower (over the 5 yr study period) than on Bermuda's outer rim reef, where water quality is exceptional and nutrient concentrations are often indistinguishable from Sargasso Sea water of the oligotrophic North Atlantic gyre (Morris et al. 1977).

Bermuda's reefs are dominated by massive, hemispherical, high-relief coral species from the *Diploria-Montastraea-Porites* coral assemblage and notably lack branching acroporid species. In the present study, BBD was observed in all of the *Diploria* spp., *Montastraea* spp. and *Porites* spp. that make up the assemblage, but prevalence levels were typically low (see also Weil 2004). BBD prevalence levels were only high enough in 1 species, *D. strigosa*, to allow spatial and temporal patterns to be examined, and because this species is the most common coral in Bermuda (with a wide distribution across the platform), the relationship between BBD prevalence and proximity to the sewage was analyzed mostly with *D. strigosa*.

Sewage pollution and BBD prevalence

Hydrological investigations around the sewage outfall, involving a combination of lagrangian and eulerian current studies, showed complex flow patterns, with weakly semi-diurnal tidal components often fluctuating on diurnal periods. Overall, the primary axis of flow was identified as a longshore current (in a NE/SW direction), and the inequality of the semi-diurnal characteristics partly results in a biased flow to the SW. This residual flow was also consequence of wind-driven patterns, where the tide, although rising and falling, occasionally ebbed and flooded in the same direction (i.e. to the SW sector, see also the supplement at www.int-res.com/articles/suppl/m462p079_supp.pdf).

The detailed hydrological studies were needed in the present study to guide the placement of monitoring sites for BBD prevalence, which were eventually located along the primary axis of flow identified from the current meter deployments. The putative gradient was examined using water sampling and counting of fecal indicator bacteria (gastrointestinal enterococci). The sampling was conducted during a calm sea-state and a flooding tide and showed elevated CFUs primarily west of the outfall rather than east and higher levels closer to the outfall than in more distant locations. These results are consistent with the finding of the hydrological studies and confirm that the sampling sites were located along a sewage exposure gradient associated with the outfall.

It was expected that if there was a relationship between BBD and sewage pollution, the prevalence would be highest on reefs closest to the outfall (which are regularly inundated by sewage) and decrease with increasing distance from the outfall. Contrary to these expectations, BBD prevalence in *Diploria strigosa* was higher further away from the outfall. The overall BBD prevalence in *D. strigosa* on reefs exposed to sewage was lower than on the northern rim reef 10 to 15 km from the nearest coastline. Although only 33 incidences of BBD were recorded in *Montastraea franksi* (in 10 500 colonies examined), no incidences were ever recorded at the sites closest to the outfall over the duration of the 5 yr study. This pattern is also consistent with there being no relationship between BBD prevalence and sewage exposure in *M. franksi*.

Spatial patterns of BBD prevalence

Diploria strigosa abundance was very low on some of the nearshore patch reefs and the inshore reefs, and BBD infections were rarely observed there. On the shallow (<10 m depth) outer rim reef and patch reefs of the lagoon, BBD prevalence levels were higher, and *D. strigosa* abundance was much higher. While this pattern suggests a positive relationship between abundance and BBD prevalence, the highest *D. strigosa* abundance in Bermuda was found on the deeper main terrace reef system, where BBD prevalence was very low. Light has been suggested as a factor controlling BBD progression (Kuta & Richardson 2002, Boyett et al. 2007), and on hemispherical or conical species, such as *D. strigosa*, BBD usually appears on flat, sunlight-exposed surfaces (Antonius 1976). This observation is consistent with multiple reports of higher BBD prevalence in shallow as opposed to deep water (Rützler & Santavy 1983, Taylor 1983, Antonius 1985). Thus, the low BBD prevalence on the main terrace could be the result of the light requirement of the photoautotrophic cyanobacteria of the BBD consortium (Kuta & Richardson 2002, Richardson & Kuta 2003). The pattern could also be due to absence of a putative BBD disease vector and also to water temperatures, which are usually cooler on the terrace reef for most of the summer (R. Jones unpubl. data).

Over the study period, the BBD prevalence in *Diploria strigosa* on the outer rim reef systematically decreased from a maximum value (per site) of 2.8% in 2004 to 0.6% in 2008. In August 2003, and during a coral bleaching event, BBD prevalence levels were as high as ~3.9% (at Site A; see Fig. 1B; see Jones 2004). BBD abundance has a strong positive correlation with temperature in field studies (e.g. Bruckner et al. 1997, Borger & Steiner 2005, Voss & Richardson 2006). In 2003, water temperatures (recorded by *in situ* temperature loggers on the reef) were unusually high, both in terms of absolute maximum temperature and also in terms of cumulative temperature, i.e. the number of days in which average daily seawater temperatures exceeded a given level. The summers of 2004 and 2005 were also much warmer than 2006, 2007 and 2008, and the general decrease in the BBD prevalence over the study period could be related to water temperatures. This could be either directly by increasing the progression and activity of pathogen, or as noted by Boyett et al. (2007), by change in other factors that vary concurrently with water temperature.

One of the more surprising results of the present study was the near absence of BBD in *Diploria labyrinthiformis* compared with *D. strigosa*. Over the study period, there were only 3 recorded incidences of BBD in just over 30 000 colonies of *D. labyrinthiformis* examined, compared to >300 incidences in just over 75 000 colonies of *D. strigosa*. Antonius (1981) indicated that *D. strigosa* was more BBD susceptible than *D. labyrinthiformis* (see also Weil 2004), but in their initial description of the disease in

Bermuda, Garrett & Ducklow (1975) made no distinction between the 2 species, citing a prevalence level of 0.5 to 1% for both. The 2 species are within the same genus and have broadly similar spatial and depth-related distributional patterns in Bermuda (Fricke & Meischner 1985, Logan 1988), and it is not clear why *D. labyrinthiformis* is almost immune to BBD infection.

Recent laboratory studies have shown that *Diploria labyrinthiformis* in Bermuda will develop the symptoms of BBD when an inoculum (from a colony of *D. strigosa*) is introduced into a surface lesion (Kuehl et al. 2011). Experimentally manipulating combinations of light and temperature will also change the rate of progression of BBD across the surface of inoculated *D. labyrinthiformis* colonies in the same way as on *D. strigosa* colonies (Kuehl et al. 2011). This suggests that the source of the differential susceptibility to BBD between the 2 species is related to factors before infections are established. Interestingly, in their recent comparative study of sexual reproduction in the genus *Diploria* (*D. strigosa*, *D. clivosa* and *D. labyrinthiformis*), Weil & Vargas (2010) noted that the morphological and micro-morphological characteristics of *D. labyrinthiformis* appear significantly different to the other species examined, with *D. labyrinthiformis* appearing similar to other taxonomically distinct species (i.e. *Dendrogyra*). Weil & Vargas (2010) recommended a reassessment of its taxonomic position, and it follows that the difference in susceptibility of *D. labyrinthiformis* and *D. strigosa* to BBD infection in Bermuda may be phylogenetic in origin.

Ecological significance of BBD in Bermuda

Bermuda's reefs are some of the most northerly and most isolated in the world. With a very high population density and with already clear evidence of local pollution (Jones 2007, 2010, 2011, Jones et al. 2011), they are in a high threat category. Some of the earliest coral reef surveys ever undertaken were conducted on Bermuda's reefs in the 1980s (see Dodge et al. 1982, Logan 1988). Although the exact locations (i.e. position within individual reefs) of these surveys are unknown, the present day cover and composition in the major physiographic reef zones in which the surveys were conducted have essentially remained unchanged. Thus, despite the threats, Bermuda's reefs have evidently fared quite well over the last quarter century compared with those of the wider Caribbean (see Gardner et al. 2003).

BBD poses a significant threat to Bermuda's reefs because it is usually always associated with tissue loss, i.e. with partial coral mortality (Edmunds 1991), and was observed on all 5 of the key coral species in Bermuda responsible for reef formation (i.e. the *Diploria-Montastraea-Porites* species assemblage). These species have massive growth forms, are resistant to hurricane and storm damage and have yet to suffer appreciable levels of mortality during bleaching events (Cook et al. 1993), and consequently, BBD infection constitutes one of the most important potential sources of natural mortality.

Offsetting the overall risks posed by BBD infection to the corals of Bermuda is the fact that prevalence levels are currently low (see Weil 2004) and largely confined to 1 species, *Diploria strigosa*. Furthermore, BBD infection is very low on Bermuda's main terrace reef system. This geomorphologcial feature (the '10 fathom terrace' of Stoddart 1969) is very well developed in Bermuda (Stanley & Swift 1968). Located at 14 to 18 m depth and extending from 1 to 7 km seaward of the rim to the outer platform margin, the terrace has a high coral cover (up to 70% in the present surveys) and forms the bulk of Bermuda's reef. It can effectively be considered a refugium from BBD infection for the *Diploria-Montastraea-Porites* species assemblage.

It is interesting to note that on the terrace, the ratio of *Diploria strigosa*:*D. labyrinthiformis* is ~3.5:1, whereas on the outer rim reef (where BBD infections are most common in *D. strigosa* but not in *D. labyrinthifomis*), the ratio is much less (i.e. <1.5:1). It is rare to find large (0.5 to 1 m diameter) colonies of *D. strigosa* on the outer rim reef without any patches of partial mortality consistent with a prior BBD infection (evidenced by smooth edged circular or elliptical patches of partial mortality, mainly on the tops and sides of colonies; see Garrett & Ducklow 1975). We speculate whether the susceptibility of *D. strigosa* to BBD infection and comparative immunity in *D. labyrinthiformis* is decreasing its competitive ability on the shallow outer rim reef and that this is an ecological signature of the effect of BBD in structuring Bermuda's reef.

In conclusion, in this 5 yr study of BBD prevalence in corals at multiple locations in Bermuda, including sites in different reef zones and along a confirmed sewage contamination gradient, there was no evidence for elevated BBD prevalence in *Diploria strigosa* in relation to sewage pollution. Overall, BBD prevalence levels were higher in areas of generally exceptional water quality characteristics of the oligotrophic North Atlantic gyre, characterized by the Sargasso Sea.

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