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Abstract
The primary building block of coral reef ecosystems, whether an isolated mid-ocean atoll or a complex system of thousands of reefs, are the individual coral colonies that combine to form the reef structures which host coral communities. The state of a coral reef community (i.e. percentage coral coverage, dominant growth forms and size classes), or any other ecosystem, at any given time is the result of interactions between a range of disturbances and routine ecological processes that operate across a continuum of spatial and temporal scales (Gunderson et al 2002). The biological (living coral colonies) and structural (dead coral framework and rubble) legacies left behind in coral communities after a disturbance influence both the vulnerability of those communities to further disturbance and their ability to maintain current community structure: ecological resilience (Nystrom and Folke 2001). While some disturbances, particularly damage from tropical cyclone waves, can affect large areas with a single event, damage is invariably patchy in distribution because vulnerability varies at many scales, from individual coral colonies upwards. Thus, disturbance regimes need to be understood at regional scales (100s of km) to capture their full extent, and at very local scales (10s of m) to assess their potential impacts. Doing so has proved difficult because direct observations of damage are typically only possible at very local scales, at which high variability obscures regional patterns (Schneider 2001). A few studies have attempted to characterise the dynamics of large, infrequent disturbances across broad regions – for example, periodic forest fires and volcanic eruptions – but only for land-based ecosystems (Turner and Dale 1998). This paper describes the first such characterisation for a large marine ecosystem, which examines tropical cyclone disturbance across the Great Barrier Reef (GBR) over 35 years (1969-2003).

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Abstract
The primary building block of coral reef ecosystems, whether an isolated mid-ocean atoll or a complex system of thousands of reefs, are the individual coral colonies that combine to form the reef structures which host coral communities. The state of a coral reef community (i.e. percentage coral coverage, dominant growth forms and size classes), or any other ecosystem, at any given time is the result of interactions between a range of disturbances and routine ecological processes that operate across a continuum of spatial and temporal scales (Gunderson et al 2002). The biological (living coral colonies) and structural (dead coral framework and rubble) legacies left behind in coral communities after a disturbance influence both the vulnerability of those communities to further disturbance and their ability to maintain current community structure: ecological resilience (Nystrom and Folke 2001). While some disturbances, particularly damage from tropical cyclone waves, can affect large areas with a single event, damage is invariably patchy in distribution because vulnerability varies at many scales, from individual coral colonies upwards. Thus, disturbance regimes need to be understood at regional scales (100s of km) to capture their full extent, and at very local scales (10s of m) to assess their potential impacts. Doing so has proved difficult because direct observations of damage are typically only possible at very local scales, at which high variability obscures regional patterns (Schneider 2001). A few studies have attempted to characterise the dynamics of large, infrequent disturbances across broad regions – for example, periodic forest fires and volcanic eruptions – but only for land-based ecosystems (Turner and Dale 1998). This paper describes the first such characterisation for a large marine ecosystem, which examines tropical cyclone disturbance across the Great Barrier Reef (GBR) over 35 years (1969-2003).

Introduction
Coral reefs are valued for their role in supporting fisheries, protecting shorelines, providing habitat for a diverse range of species, and attracting tourists. Recognition of these values in the face of increasing human use has led to efforts for their protection, such as the establishment of marine protected areas in which destructive human activities (mineral extraction) are banned and other human uses (fishing, tourism) are restricted temporally and spatially. To evaluate the effectiveness of regulation of the human use of reefs, it is also important to understand the spatial and temporal characteristics of unmanageable impacts like those caused by tropical cyclone-generated waves.
Disturbances have always been a part of the environment of coral reefs. However, their impacts on coral reef ecosystems are poorly characterised (Hammer and Wolanski 1988, Done 1992a, Sebens 1994). The degree to which reef community structure and function will be altered by disturbances depends not only on the type, intensity, extent, timing, and frequency of the disturbances (Lirman and Fong 1997, Nystrom et al 2000), but also on the nature of the coral communities themselves (Done 1992b), which can vary significantly across small distances due to zonation and patchiness (Done 1983) and over short time periods due to 'routine mortality' (Hughes and Connell 1999). Thus, at the local scale, quantitatively assessing the impact of a given disturbance requires very detailed information about the patchy mosaic of the target community and the reef conditions present at the site (including the recent history of disturbances) before and after the disturbance. This type of data (Connell et al 1997) is very time consuming and costly to gather, is still very limited and is never likely to be obtainable except by serendipity, and then at very local scales. A more tenable goal is the characterisation of the natural disturbance regimes that affect reef areas. The major natural disturbances that affect the GBR region include: broad-scale bleaching (Berkelmans 2002), crown-of-thorns starfish predation (Moran 1986), exposure to fresh water plumes during flood events (King et al 2001), and physical damage from tropical cyclone generated waves (Massel and Done 1993). The continued existence of coral reefs despite repeated exposure to cyclone waves over thousands of years indicates their resilience to this form of disturbance. However, it has been shown that when natural disturbances to reefs are combined with human-induced damage (ie overfishing in Jamaica – see Hughes 1994), reef communities may undergo permanent change. Thus, designing effective management strategies for reef conservation requires understanding patterns in both human-induced and natural disturbances, as well as how they interact over multiple time and space scales.

While many studies have examined damage from particular cyclones on specific reefs, very few studies have considered more than a single cyclone and more than a single reef at a time. To date, very few attempts have been made to model a cyclone disturbance regime. Woodley (1992) did so for a single site in Jamaica and Treml et al (1997) for several sites in the Lesser Antilles. Both used only the distance to a cyclone's path as a proxy for disturbance potential, which has been shown to be inadequate (Puotinen 2005a). Indeed, deeper understanding of the potential implications for reef recovery from cyclones requires modelling the regime across entire regions of interconnected reefs. To fill this gap, a project was developed to characterize the tropical cyclone disturbance regime across the entire GBR using meteorological and ecological models within a Geographic Information Systems (GIS) framework, reconstructing a probable cyclone disturbance history of the region over the past 35 years (1969-2003).

**Methods**

*Defining reef sites*

Characterising the tropical cyclone disturbance regime in the GBR required modelling the distribution of cyclone energy at broad scales (100s of km at a 1 km resolution) and the vulnerability of coral communities at local scales (individual sites within each reef), because vulnerability to cyclone damage can vary between sites located only hundreds of metres apart. To capture this local scale variability, a series of ‘sites’ were defined around the perimeter of each reef at a 1 km interval (Figure 1) at which to model the cyclone disturbance regime. For the 2,728 individual reefs of the GBR, this produced a total of 24,224 individual sites. Although each site is indicative of the local exposure conditions in its vicinity, high variability in vulnerability across very small distances means that it is not representative of the entire 1 km area.
Reconstructing the tropical cyclone disturbance history

Very little field data documenting cyclone damage of sites and actual measurements of wind and wave energy exists for the GBR. Thus, the first step in the project was to reconstruct a cyclone disturbance history from the information that was available. This involved: 1) hindcasting the distribution of cyclone energy for the past 35 years (1969-2003), 2) modelling reef exposure and vulnerability to that energy, 3) linking measures of cyclone energy and reef vulnerability to patterns in known cyclone damage to reefs, and 4) using the resultant model to predict cyclone damage at each of 24,224 sites identified around the reefs for each of the 85 cyclones that passed nearby during the time series. Meteorological equations implemented in a Geographic Information Systems (GIS) were used with data from the Australian Bureau of Meteorology to reconstruct the spread of high winds and wind directions (as a proxy for the potential formation of heavy seas) around the cyclone eye every hour along its path. This was done for each of the 85 cyclones that passed near the GBR from 1969 to 2003 (Puotinen 2005b). The resultant data was then used to derive three cumulative measures of cyclone energy over the life of each cyclone: maximum wind speed, duration of gale force winds, and continuous duration of gale force winds (Puotinen 2005c). Together, these parameters give an indication of the maximum wave conditions that were possible during each cyclone.
However, waves lose much of their energy when breaking at the leading edge of the first reef (or other shallow water obstacle) they encounter (Young and Hardy 1993), creating a shelter effect where the lee side of the reef receives relatively little wave energy, and reefs beyond the first obstacle lie within a low energy 'wave shadow'. Thus, some sites located in areas where cyclone winds (and thus waves) were intense may not have been exposed to the heavy seas capable of damage. This was modelled by measuring the distance to the nearest potentially wave-blocking obstacle (islands, reefs, coastline, water < 50 m deep) in all directions around each site at an interval of 7.5 degrees (see Puotinen 2003). These distances provided a crude measure of fetch (the distance over which winds can blow uninterrupted to build waves) around each site. Exposure to incoming wave energy during each cyclone was estimated by averaging the fetch distances found within 45 degrees of the dominant incoming wind direction during that cyclone. Routine levels of wave exposure were compared to this to estimate the level of relative exposure (how much more exposed the site was during the cyclone than normal). The structural vulnerability of each site was also considered by examining the geomorphologic type of each reef, its habitat (high energy front versus low energy back), the water depth and the slope (Puotinen 2005e).

Classification and regression tree (CART) analysis was then used to determine how well observed patterns in wave damage (taken from three field surveys of cyclone damage to GBR reefs: cyclones Ivor and Joy, 1990 and cyclone Justin, 1997 – see Puotinen 2005a) could be explained by the potential explanatory factors described above. The advantage of using this approach for this study, as opposed to logistic regression or other standard techniques, was its ability to handle both numeric and categorical data, multi-level categorical variables, missing observations, and data that does not meet the assumptions of standard parametric tests (De’ath and Fabricius 2000). CART was used to search for meaningful structure in the data, and to derive decision rules to predict the occurrence of different types of damage across the GBR during each of the cyclones in the study period (see Puotinen 2003, 2005e). Four measures of cyclone wave damage were successfully modelled: the presence or absence of coral breakage, dislodgement of colonies from the reef substratum, exfoliation (peeling back of the reef framework) and severe damage of any type (Table 1).

Subsequently, descriptors of the cyclone disturbance regime (described in next section) were calculated for each site. To identify broad trends in the latter, the GBR was divided into one-degree latitude by one-degree longitude blocks, within which values for the reef sites were averaged. In this paper, results are presented only for severe damage of any type (see Puotinen 2005d for results for the remaining three damage types).

**Characterising the disturbance regime**

The dynamics of a disturbance regime can be described using a range of interrelated descriptors, such as the frequency, return interval, and magnitude of the disturbance (White and Pickett 1985). In this paper, two basic descriptors (incidence and timing) illustrated by four calculated parameters (time series plots, number of disturbance-free periods, mean length of disturbance-free periods, maximum length of disturbance-free periods, time since last event) are presented for one of the modeled damage types: severe damage of any type.
Table 1: Decision rules for predicting the occurrence of four types of cyclone damage across the GBR from 1969-2003, and the cyclone damage field survey data on which they are based. Separate rules were used for cyclone Justin in some cases due to its unusual properties (see Puotinen 2005a).

<table>
<thead>
<tr>
<th>Type of damage</th>
<th>Data set(s)</th>
<th>Decision Rules</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence or absence of severe damage of any type</td>
<td>Ivor, Joy, Justin</td>
<td>Impacts are severe IF: maximum winds &gt; 25.3 m/s and slope = moderate; or IF: maximum winds &gt; 25.3 m/s and slope = flat and distance &gt; 28.2 and habitat = front.</td>
</tr>
<tr>
<td>Presence versus absence of coral breakage</td>
<td>Ivor and Joy</td>
<td>Breakage is present IF: distance &gt; 33.1 km, and duration of gales &gt; 53.5 hours and habitat = front; or IF: distance &gt; 33.1 km and duration of gales &gt; 33.5 hours and habitat = back and reef type = crescentic, incipient fringing, ribbon or submerged.</td>
</tr>
<tr>
<td>Presence versus absence of dislodgement of massives</td>
<td>Ivor and Joy</td>
<td>Dislodgement is present IF: distance ≤ 78.1 km.</td>
</tr>
<tr>
<td>Presence versus absence of exfoliation</td>
<td>Ivor, Joy, Justin</td>
<td>Exfoliation is present IF: habitat = front and maximum winds &gt; 24.7 m/s.</td>
</tr>
</tbody>
</table>

The incidence of a disturbance indicates the proportion of area affected by it. For cyclones on the GBR, this was measured by calculating the percentage of reef sites at which wave damage was predicted to occur during each cyclone.

The timing of cyclone disturbances in the GBR was examined based on: 1) the number of disturbance-free intervals, 2) the mean number of years expected between successive disturbances (return interval) and 3) the maximum length of disturbance-free intervals, and 4) the number of years since the last cyclone event. These were measured for the GBR by constructing a spreadsheet of cyclone events from 1969 to 2003, noting predicted damage (value of 1) or not (value of 0) for each of the reef sites, and counting the number of disturbance-free intervals, as well as measuring the length (in years) of each one (see Puotinen 2004b, 2005c).
Results

Incidence

Just over half (55%) of cyclone events over the past 35 years were predicted to be capable of causing severe damage of any type (Figure 2). Of these, five could have affected more than 25% of GBR reef sites. These include cyclones Althea (1971), Fiona (1971), Alan (1976), Paul (1980) and Ivor (1990). Some of these events may over-predict cyclone energy due to high cyclone translation speeds, which reduce the accuracy of the wind modeling (Puotinen 2005b).

The potential for cyclone disturbance at the reef sites was generally intermittent. Cyclone events were rarely predicted to affect more than a quarter of the sites at once. However, no unusually large and strong cyclones, which would have the potential to disturb a large proportion of the GBR at once, passed nearby over the past three decades. Further, very strong cyclones located too distant from the GBR to be considered in this study could have damaged a large number of the outer reef sites with long-period ocean swell. For example, storm surge was recorded during cyclone Pam in 1974 (Hopley and Harvey 1974) along the entire Queensland coast south of Cairns when the cyclone was located hundreds of km from the GBR.

Figure 2: Percentage of GBR sites predicted to be affected by severe damage of any type for each cyclone event from 1969 to 2003 (no cyclone events occurred after 2000). In the absence of habitat data for most sites, half were assumed to be fronts and half to be backs. These results assume that a susceptible slope exists at each site. Cyclones predicted to have damaged more than 25% of GBR sites include: 1 – Althea 1971, 2 – Fiona 1971, 3 – Alan 1976, 4 – Paul 1980, and 5 – Ivor 1990.

Timing

Between six and eight intervals free of severe damage of any type (Figure 3-A) were predicted for the GBR, with no clear trend with change in latitude or longitude. The mean length of severe damage-free intervals (Figure 3-B) is generally similar across the region (range = 3-6 years), with the longest intervals found north of 10°S. The maximum number of years between severe damage (Figure 3-C) was 13, with an
average of 10 across all the sites. The distribution of the longest maximum intervals was patchy across the GBR. Severe damage of any type was generally predicted to occur most recently (in 1998) for sites situated from $15^\circ$S-$16^\circ$S (Figure 3-D), though sites located at $22^\circ$S, $151^\circ$E (offshore Rockhampton) and $23^\circ$S, $150^\circ$E (close to the coast north of Gladstone) were disturbed even more recently (2000).

Figure 3:  Severe (widespread) damage of any type. Patterns in severe damage of any type across the GBR from 1969 to 2003:  A – number of severe damage-free periods, B – mean length of severe damage-free periods, C – maximum length of severe damage-free periods, and D - number of years since the last severe damage (as of 2003), averaged in each $1^\circ$ latitude by $1^\circ$ longitude box. The colour of each box indicates the relative number of years: white $= <10$, light grey $= 10$-$20$, dark grey $= 20$-$30$, black $= >30$.

Sites situated between $18^\circ$S-$19^\circ$S were predicted to be severely damaged least recently, with the last event between 11 and 13 years ago. The number of years since the last severe damage (Figure 3-D) was never less than the mean predicted number of years between successive events (Figure 3-B), though one instance it was equal (in the far southern GBR). The number of years since the most recent cyclone event (as measured from 2003) was usually greater than the median number of years between successive
events over the time series. This suggests that reef sites have been less disturbed recently than what was typical over the past 35 years.

Massel and Done (1993), based on cyclone positions from 1910-1980, predicted that cyclones of all intensities return more frequently to latitudes from about 19°-23°S. That trend was not evident in this analysis, suggesting that the cyclone disturbance history over the past 35 years (1969-2003) may not be typical of what occurred further in the past (1910-1968). It also may reflect large known uncertainties in the positioning of cyclone paths and their detection in the time series prior to 1969 (Holland 1981). Interestingly, sites located around 19°S were typically disturbed the least recently, even though several cyclones have passed through that area in recent times (they were relatively weak). This highlights the inadequacy of considering the proximity to the cyclone path alone as well as the need to model intensity.

Figure 4: Effects of cyclone disturbance regimes on the extent of coral coverage and dominant colony size (thick black line) over decades (adapted from Done 1992a and Dollar and Tribble 1993). As the time since the last disturbance increases, coral coverage and the dominant colony size increase until crowding results in biological interactions that reduce species diversity. In A, the maximum coverage that can be supported in the available space is reached. In B, periodic major disturbance reduces coral coverage and colony size before the maximum can be reached. In C, the timing of intermittent minor (C2) and severe (C1 and C3) disturbances determine whether and for how long the maximum is reached. Note that the colony size – disturbance relationship is more complex for massive corals and in general has a more gradual slope than shown here.
Implications for Coral Reef Communities

The frequency, timing and severity of cyclone damage on reef sites can play a major role in determining their structure. Thus, the cyclone history has implications for coral community structure, such as the level of coral coverage (Figure 4). For example, reef sites that are frequently damaged (at intervals of less than 10 years) are likely to be characterised by low coral coverage and dominated by smaller sized colonies for much of the time. In contrast, reef sites that are damaged at intermediate intervals (one to several decades) are at times left undisturbed long enough for high coral coverage and large sized colonies to dominate. The extent to which this is true at a given time period will depend on the length of time since the last severe cyclone disturbance relative to the typical interval.

For the GBR, the nature of the cyclone disturbance history predicted from 1969-2003 for severe damage of any type can be classified as high or intermediate based on the timing of cyclone damage and the number of years estimated to be required for recovery of coral communities to their prior state (Table 2).

Table 2: Summary of the predicted timing of cyclone disturbance (as predicted for severe damage of any type) in the GBR from 1969 to 2003.

<table>
<thead>
<tr>
<th>Type of damage</th>
<th>Estimated time to recover</th>
<th>Typical return times</th>
<th>Years since last event</th>
</tr>
</thead>
<tbody>
<tr>
<td>Severe damage of any type</td>
<td>Decades to centuries</td>
<td>Short (≤ 5 years) for entire GBR. Mean = 3</td>
<td>Medium (6-13 years), with no clear pattern across the GBR. Mean = 10.</td>
</tr>
</tbody>
</table>

The mean cyclone-free interval (return interval) for the period 1969-2003 indicates the average number of years that coral communities had to recover following cyclone events in that period. If the time needed for recovery was shorter than this interval, sites generally had time to recover from one disturbance before the next one hit (intermediate disturbance). If the time needed for recovery was longer than the return interval, sites did not always have enough time to recover. In the latter case, disturbance would still be intermediate as long as the maximum interval between disturbances was sufficient for sites to recover at least once during the study period. If not, disturbance would be high as sites would never have time to fully recover.

Based on this rationale, severe damage of any type appears to be high (frequent) disturbances. It is important to note, though, that this represents a worst-case scenario because vulnerability factors have not been mapped for most of the GBR and could not be used in predictions. Including these factors would likely decrease the frequency of disturbance-free intervals and increase their lengths for the GBR overall, though it is unclear how this would vary across the region. Further, the first period in the time series for most of the sites is a minimum estimate because the earliest cyclone damage event occurred before the start of the study period. Give this, as well as indications that fewer cyclones tracked near the GBR prior to 1969 (albeit based on data of dubious quality, see Puotinen 2004a), it is possible that the maximum intervals could be longer than reported for some sites. It is also possible that recovery times could be shorter than
those predicted. Given this, severe damage of any type may actually be an intermediate disturbance.

Across most of the GBR, the latest event occurred much longer ago (as measured from 2003) than was typical over the time period 1969-2003 (Figure 5). When a much longer time period (90 years) was considered for many fewer sites (211 versus 24,224), and using a much simpler analysis (Puotinen 2004b), only reef sites located between 19-21°S were predicted to be disturbed less frequently than normal in recent times, due to a hotspot of cyclone tracks in the central GBR near Townsville (18-19°S at 147°E, see Puotinen 2004b).

**Figure 5:** Patterns in the timing of the most recent disturbance-free interval for severe damage of any type across the GBR from 1969 to 2003. The mean disturbance interval was subtracted from the number of years since the last disturbance, averaged in each 1° latitude by 1° longitude box. The colour of each box indicates whether the result was positive (white): disturbed less recently than normal, negative (black): disturbed more recently than normal or zero (grey): disturbed at the median interval.

This occurred despite the generally increased number of cyclones detected (due to improved observation techniques) tracking near the GBR from 1970 to the present compared to the rest of the time series (see Puotinen 2004b) and the fact that the first disturbance-free interval for many of the sites may represent a minimum estimate. However, the degree to which cyclones were undetected earlier in the time series due to limitations of observation techniques is unknown. Because cyclones rarely form close to the equator (due to the lessening of the Coriolis Effect), the potential for missing observations early in the time series may be less of an issue for the far northern GBR. Regardless, these results suggest that these reef sites, as currently observed, have had more time to recover from the last cyclone disturbance than normal and thus could be expected to have fully recovered and perhaps reached a ‘mature’ state. The degree to which the latter actually occurred depended on the effects of other disturbances and...
routine ecological processes (i.e. competition, growth rates) at each site since the last cyclone disturbance.

The state of a coral reef community at any given time is shaped by the complex interplay between a range of disturbances (coral bleaching, crown-of-thorns starfish predation, tropical cyclone waves) and routine ecological processes (competition, recruitment, recovery) that act across a range of spatial and temporal scales. From a management perspective, understanding the extent of human disturbances (fishing pressure, pollution) that a coral community can sustain before 'phase shifting' to a non-coral dominated state (ecological resilience) is necessary to devise long-term conservation strategies. An examination of the dynamics of each disturbance that affects a given community, as well as how they interact across time and space scales, is necessary to estimate these thresholds. The research project described in this paper provides a first step towards this goal by characterizing the dynamics of the tropical cyclone disturbance regime in the GBR.

Given that this analysis was based on only three comprehensive field surveys of cyclone data to reefs, there is considerable scope for improving the predictive model used to construct the cyclone disturbance history through a regular program of wave damage field surveys following future cyclones. To this end, a field survey of wave damage from cyclone Ingrid, which passed through the far northern GBR (~13°S) in March 2005, is due to take place in May 2005. The modeling would also be improved by the deployment of additional instrumentation to measure wave heights and directions (particularly in the far northern GBR), as this would allow calibration of modeled winds with the waves that actually cause damage to reefs. Finally, both the frequency and intensity of cyclones impacting coral reefs may increase with global warming (Pitcock 1999). The potential implications of this for the GBR could be explored by simulating a range of possible cyclone disturbance regimes based on cyclone tracks and intensities predicted from global climate change models (Henderson-Sellers et al 1998, Walsh and Pitcock 1998).

References


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