Mass mortality following disturbance in Holocene coral reefs from Papua New Guinea

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ABSTRACT

The frequency and intensity of disturbance on living coral reefs have been accelerating for the past few decades, resulting in a changed seascape. What is unclear but vital for management is whether this acceleration is natural or coincident only with recent human impact. We surveyed nine uplifted early to mid-Holocene (11,000–3700 calendar [cal] yr B.P.) fringing and barrier reefs along ~27 km at the Huon Peninsula, Papua New Guinea. We found evidence for several episodes of coral mass mortality, but frequency was <1 in 1500 yr. The most striking mortality event extends >16 km along the ancient coastline, occurred ca. 9100–9400 cal yr B.P., and is associated with a volcanic ash horizon. Recolonization of the reef surface and resumption of vertical reef accretion was rapid (<100 yr), but the post-disturbance reef communities contrasted with their pre-disturbance counterparts. Assessing the frequency, nature, and long-term ecological consequences of mass-mortality events in fossil coral reefs may provide important insights to guide management of modern reefs in this time of environmental degradation and change.

Keywords: coral reefs, disturbance, Quaternary, mass mortality, Holocene, Papua New Guinea.

INTRODUCTION

The accelerating demise of living reefs threatens their existence (Wilkinson, 2004). The degree to which this degradation is related to increased anthropogenic influences, such as overfishing (Jackson et al., 2001; Pandolfi et al., 2003), eutrophication (Lapointe et al., 2004), and climate change (Hughes et al., 2003), or the result of natural variations in population structure and climate is a major issue in the conservation strategy of coral reefs. One hypothesis is that recent human activities have resulted in increased disturbance frequencies compared with prehuman time. For reef managers interested in whether changes on living reefs are attributable to human impacts, the fossil record provides critical data on long-term natural changes before human influences.

Here we present evidence that four event horizons preserved in the Holocene raised coral reef terrace of the Huon Peninsula, Papua New Guinea, record coral mass mortality that decimated reefs along tens of kilometers of coast. These fossil sequences allow us to document the nature and frequency of disturbance and recovery in Quaternary coral reefs where human impacts were nil. We show that such events were rare for fossil coral reefs of the Huon Peninsula, but when large-scale disturbance occurred, recovery was swift and complete.

METHODS

Study Site

Using scaffolding, we surveyed eight seacliff sections and one inland section of the tectonically uplifted Holocene terrace along 27 km of the Huon Peninsula, Papua New Guinea (Fig. 1; see Data Repository Table DR1[1]), in an area of low historical and present human population. The present climate is relatively uniform, with a seasonal sea surface temper-

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[1]GSA Data Repository item 2006211, Tables DR1–DR3 and Figures DR1 and DR2 (locality, stratigraphic logs, and description of seacliffs; sampling protocol for paleoecological surveys; details of radiocarbon-dated samples; foram species abundances; and Bonah River seacliffs), is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

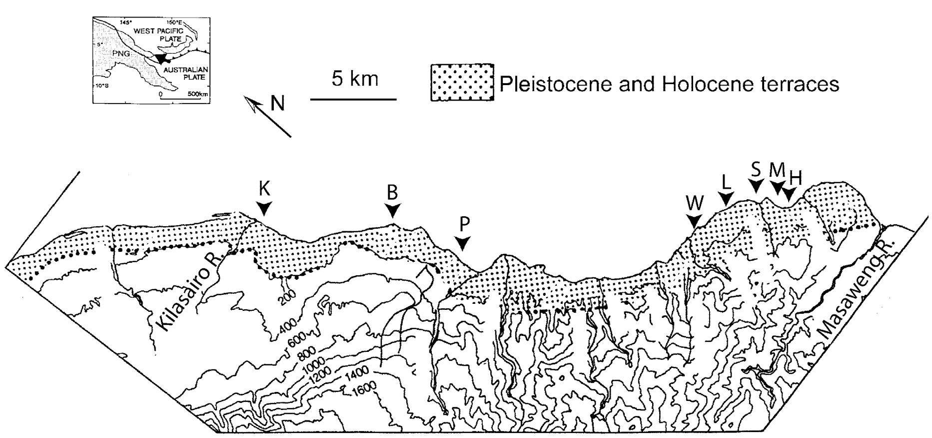

Figure 1. Map of Huon Peninsula, Papua New Guinea (PNG). Arrows point to localities studied in uplifted Holocene seacliffs. K—Kilasairo River; B—Bonah River; P—Pukau; L—Loto Beach; S—Sang River; M—Midway Cove; H—Hubegong dive site; W—Wondakai.

ature range of ~2 °C around a mean of ~29 °C, and few major storms and no cyclones. The climate during the Holocene was broadly similar to present, although interannual variability related to the El Niño Southern Oscillation was reduced (Tudhope et al., 2001). Shallow-water fore-reef deposits exposed in uplifted seacliffs as high as 24 m contain reef coral assemblages that grew between ca. 11,000 and 6400 calendar (cal) yr B.P. during the sustained sea-level rise of the last deglaciation. Most corals accumulated in place (upright, whole, and in life position), preserving both their former biological inhabitants' paleoecological histories and physical environments.

Geochemistry and Geochronology

To determine the ages, frequency, and geographic scale of individual event horizons, we collected from one to three unaltered corals and molluscs from every vertical meter of exposed Holocene seacliff for ^{14}C age dating using accelerator mass spectrometry. The ^{14}C reservoir effect for the Huon Peninsula, calculated as 407 ± 52 yr (Edwards et al., 1993), was subtracted from the conventional ($\delta^{13}C$ corrected) ^{14}C ages; the values were then converted to calendar yr B.P. (1950) using the intcal04.14c calibration data set (Reimer et al., 2004) via the CALIB program (Stuiver and Reimer, 1993).

Paleoecological Surveys

To determine the degree to which event horizons affected community composition, we completed paleoecological surveys of the fossil reefs at the Bonah River section before, during, and after one of the widespread event horizons. Horizontal line-intercept transects (Loya, 1972), 25 m long, were placed 50 cm below and at the event horizon, and then 7 transects were placed at 1 m vertical increments above the horizon (Fig. DR1; see footnote 1). To characterize the entire preservable reef fauna we targeted the corals, molluscs, foraminifera, and calcareous algae (sampling protocol, taxonomic scale, and diversity are in Table DR2; see footnote 1).

Figure 2. Major characteristics of coral reef mass-mortality events. A: Section revealing extensive mortality of *Acropora palifera* along single horizon at Bonah River (scale bar is 50 cm). B: Volcanic ash settled above and within branches of *Acropora* at Pukau (ruler is 17 cm long). Fine-grained, semiconsolidated tephra collected from ca. 9100–9400 calendar yr B.P. ash layer is almost entirely composed of transparent, greenish-tinted volcanic glass shards. C: Thick encrustation of coralline algae on branch of dead *A. palifera* at event horizon at Loto Beach (scale is 3.6 cm long). D: Section at Hubegong dive site showing coral growth above submarine debris flow (pole is 50 cm high). R. is river.

DATA ANALYSIS

We plotted percent relative abundance values of the most abundant taxa at the Bonah River section to ascertain taxonomic differences between pre-disturbance and post-disturbance communities. At the Bonah River section, a census of only one community could be taken below the event horizon because it occurred so low in the seacliff section; thus, the pre-disturbance community is compared graphically with the mean (and standard error) of the seven post-disturbance communities (Fig. DR1; see footnote 1). All the post-event survey data come from a physical environment that is very similar to the pre-event conditions in terms of water depth, location on reef, and climate.

Frequency of event horizons was calculated as the number of events pooled over the eight shallow fore-reefsites divided by the pooled stratigraphic range of the cliff sections in calendar years. We left out the youngest event horizon in the lagoonal facies at Bonah River because it was the only section studied with an age that was younger than 6400 yr B.P.; including it would lead to underestimating recurrence time based on a single sample.

RESULTS

During our seacliff surveys we observed multiple laterally continuous, subhorizontal event horizons, traceable for as much as 50 m, that shared characteristics of coral growth, algal abundances, and sedimentological anomalies that were absent from horizons above and below. There are 4 event horizons at 8 localities along the 27 km coastal survey (Fig. DR2; see footnote 1). Along these event horizons, abundant, commonly branching, in-place corals ceased growth collectively (Fig. 2A). In many places, a volcanic ash is present within the horizon (Fig. 2B). In some places a few large (>1 m diameter), usually massive, coral colonies, primarily the genus *Porites*, extended below and above the horizon. The most characteristic feature of the event horizons is extensive coralline algal and microbial micrite encrustation of the dead coral surfaces. In places this forms an almost continuous layer as much as 10 cm thick (Fig. 2C). Above the encrustation zone, there is commonly an accumulation dominated by coral rubble and sand, possibly from breakage and reworking of dead branching colonies exposed on the seabed. This zone (as thick as 50 cm) is gradually replaced upward by a more normal reef framework represented by in situ corals and associated skeletal sand and gravel.

Two of the event horizons were associated with a distinct volcanic ash layer. A 20-cm-thick ash at the Bonah River lagoon site is dated (by ^{14}C dating of enclosed skeletal material) as 3700–4000 cal yr B.P. The other ash, observed at Midway Cove, Loto Beach, and Pukau, and associated with the most widespread event horizon in the area (Fig. 3), is dated as 9100–9400 cal yr B.P. It occurs as a 1–5-cm-thick layer draped in and among the branches of the uppermost corals that collectively ceased growth. This event was contemporaneous with event horizons at the Wonda-

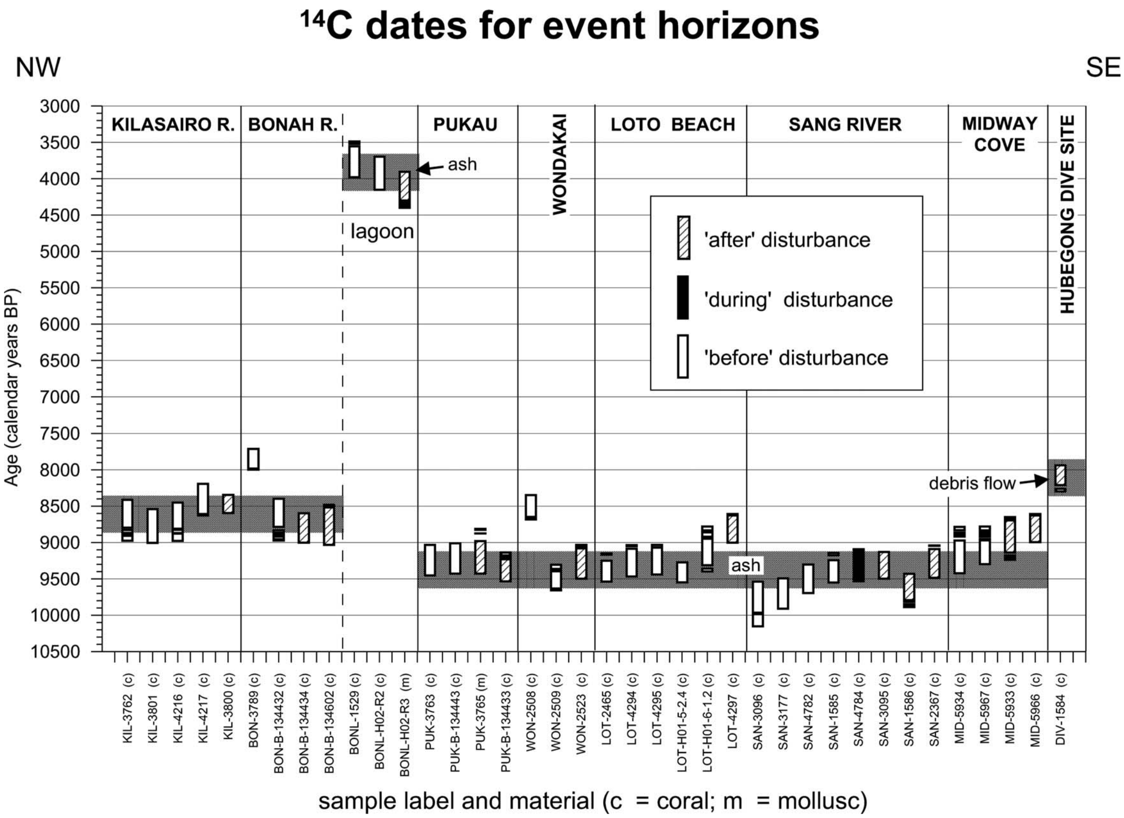

Figure 3. ^{14}C dates of event horizons along 27 km of Holocene raised reef terrace from Huon Peninsula, Papua New Guinea. Two widespread event horizons are dated as ca. 9100–9400 calendar yr B.P., and ca. 8500 calendar yr B.P. Isolated examples of coral mortality were observed in Bonah River lagoon and Hubegong dive site. Event horizons are shaded, and labeled with their likely cause where this has been deduced (ash = associated with volcanic ash layer, or debris flow = associated with a submarine debris flow). Shown here are 2 sigma age ranges in calendar yr B.P. Data for each sample are found in Table DR3 (see footnote 1).

kai and Sang River sections (Fig. 3), suggesting that here too volcanic ash may have been the causative agent, but there was poorer preservation of a discrete ash horizon.

A third event horizon occurred at the Hubegong dive site, where the top portion of a submarine debris flow was dated as 7938–8298 cal yr B.P. (Figs. 2D and 3), which temporarily halted reef growth before the reef recolonized. This is slightly younger than the fourth event horizon at Kilasairo and Bonah River, dated as ca. 8500 cal yr B.P. (Fig. 3).

To estimate the frequency of the event horizons in our study area, we note that in the 8 coastal cliff sections representing growth of upper fore-reefslope communities, there are 3 event horizons in the interval 11,000–6400 yr B.P. (age range of all sections). This equates to an average of 1 event per 1500 yr.

At the lower Bonah River section (Fig. 1), the majority of coral, gastropod, and coralline algal species show pre-disturbance abundances outside of the error bars of post-disturbance communities (Fig. 4). The abundance of *Acropora palifera* and arborescent *Acropora* was very high before the horizon, but low afterward (Fig. 4A). In contrast, species from the *A. hyacinthacis* and *A. humulis* groups were rare before the horizon, but abundant afterward (Fig. 4A). Other corals became established only after the event horizon. The pre-event gastropod assemblage has a much lower abundance of *Turbo* species compared with after the event (Fig. 4B). Abundance data for foraminifera, taken from only four transects after the disturbance, show high variability but no trends through time (Fig. DR1; see footnote 1). The taxonomic composition of coralline algae was characterized by greater abundance of *Porolithon onkodes* before and during the disturbance versus after (Fig. 4C).

DISCUSSION

The ecological, physical, and sedimentological characteristics of the four event horizons on the Huon Peninsula are consistent with coral mass-mortality events. Destruction of large areas of Holocene reef resulted in the simultaneous death of >90% of the corals. Subsequent reef growth was initially confined to algal encrustations.

The ca. 9100–9400 cal yr B.P. mass-mortality episode was the most widespread and is associated with a volcanic ash (Fig. 3). Coral mortality was caused by smothering, presumably following direct air fall and possibly during subsequent reworking of the terrestrial volcanic ash onto the reef (cf. Heikoop et al., 1996; Genin et al., 1995). It occurs along 16 km of coast and includes 5 of the sections (Fig. 3). A second widespread event is dated as ca. 8500 cal yr B.P., and is not associated with a volcanic ash layer. It was observed at Kilasairo and Bonah River (Figs. 1 and 3). Zones without ash may have lost such deposits to scouring by waves, or mortality may be due to other processes.

The mean frequency of Holocene mass-mortality events we observed is only ~1 disturbance per 1500 yr. Each of these events was easily recognizable in the distinctive sedimentary signature left in the accumulating reef. Although it is likely that other, smaller, disturbance events occurred within the time frame (e.g., less widespread and/or with only partial coral mortality), we believe that it is unlikely that there were other major mortality events. Three of our identified events appear to be related to factors that are exogenous to the reef system (two ash falls and one marine debris flow). The origin of the fourth event is unknown. We conclude that for these reefs at least, outside of the zone of cyclones and major storms, large-scale mass mortality occurred infrequently, and in most cases was related to an easily identified external factor.

This pattern of infrequent mass mortality in the Holocene reefs is in marked contrast to some modern, human affected, reefs where much more frequent and widespread mass-mortality events are well documented (e.g., Wilkinson, 2004). Recent mass-mortality events that are equivalent in magnitude to the four recognized in the fossil record in the present study include any disturbance that results in the simultaneous die-off of a large majority of live corals on patches distributed over a spatial scale of tens of kilometers. The primary agents of these disturbances include coastal eutrophication, hurricanes, disease, bleaching events, and crown-of-thorns starfish outbreaks. As an example, many sites in the

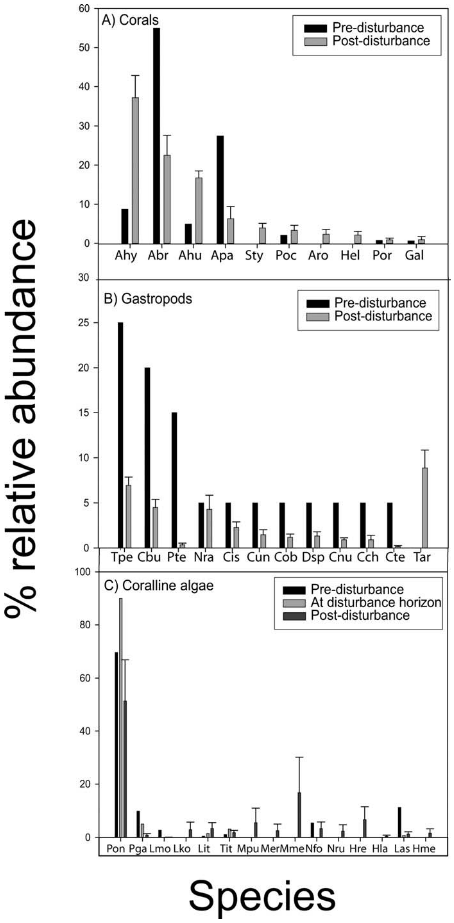

Figure 4. Percent relative abundance of major reef organisms before, during (coralline algae only), and after 8500 calendar yr B.P. mass-mortality event at Bonah River section at Huon Peninsula, Papua New Guinea. Error bars are standard error of mean for seven post-disturbance transects. A: Coral species composition. Ahy—*Acropora hyacinthus* species group; Abr—arborescent *Acropora*; Ahu—*A. humulis* species group; Apa—*A. palifera*; Sty—*Stylophora*; Poc—*Pocillopora*; Aro—*A. robusta* species group; Hel—*Heliopora*; Por—*Porites* spp.; Gal—*Galaxaea*. B: Gastropod species composition. Tpe—*Turbo petholatus*; Cbu—*Cypraea bulla*; Pte—*Pyrene testudinaria*; Nra—*Neritopsis radula*; Cis—*C. Isabella*; Cun—*Cantharus undosus*; Cob—*Conus balteatus*; Dsp—*Diodora* sp. 1; Cnu—*Cypraea nucleus*; Cch—*C. childreni*; Cte—*C. teres*; Tar—*T. argyrostomus*. C: Coralline algal species composition. Pon—*Porolithon onkodes*; Pga—*P. gardineri*; Lmo—*Lithophyllum moluccense*; Lko—*L. kotschyanum*; Lit—*Lithoporella melobesioides*; Tit—*Titanoderma* sp.; Mpu—*Mesophyllum purpurascens*; Mer—*M. erubescens*; Mme—*M. mesomorphum*; Nfo—*Neogoniolithon fosliei*; Nru—*N. rufum*; Hre—*Hydrolithon reinboldii*; Hla—*H. laeve*; Las—*Lithothamnium asperulum*; Hme—*H. megacystum*. Plotted are 10 most abundant corals (96% of occurrences), all 11 gastropods found in pre-disturbance community plus most abundant of remaining gastropods (33% of post-disturbance occurrences), and all of coralline algae species.

Caribbean Sea have undergone repeated disturbance and community change related to overfishing, eutrophication, hurricanes, and loss of herbivores due to disease, all within the past few decades (Hughes and Connell, 1999). Although there are some clear differences between these Caribbean reef systems and our Papua New Guinea example, our data take an initial step toward helping place recent reef disturbance and mortality events in the context of natural rates in pristine reef systems.

The decadal to centennial resolution of disturbance events in the Quaternary coral reef record enables coupling of disturbance regimes with changes in community composition. Tight clustering of age dates obtained around mass-mortality events attests to the rapid recovery ($<$100 yr, perhaps even decades; see Fig. 3) of the reefs, whose accretionary rates were comparable to pre-disturbance levels. A phase shift from coral to algal-dominated reef occurred immediately following the mass-mortality events, but coral assemblages quickly recolonized. The thick coralline algal encrustations may have facilitated subsequent coral recruitment, as in modern reef settings (Harrington et al., 2004). Recovery of some modern reefs has also been shown to be rapid (Connell, 1997), but these Quaternary data demonstrate that rapid recolonization can swiftly lead to a fully functional reef community capable of renewed reef accretion following disturbance.

Although the general applicability of our ecological results must be viewed as tentative until data can be analyzed from other sections along the coast, it is interesting to note that the taxonomic composition of coral, gastropod, and coralline algae communities differed before and after the disturbance event at Bonah River (Fig. 4). Furthermore, some of these differences persisted for at least 2000 yr of post-disturbance reef accretion. Further analysis of Holocene reefs from Huon Peninsula will provide reef managers with a temporal context for understanding the degree to which reef communities are randomly assembled or the product of a long process of succession, the relative importance of species incumbency, and the long-term effects of disturbance on coral reefs. Recognition of past coral mass mortality now opens the exciting possibility of examining changes in reef community structure, accretion rates, and coral growth through time under varying disturbance regimes and using them to predict the effects of disturbance on modern coral reefs.

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