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Predicted recurrences of mass coral mortality in the Indian Ocean

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In 1998, more than 90% of shallow corals were killed on most Indian Ocean reefs[1]. High sea surface temperature (SST) was a primary cause[2,3], acting directly or by interacting with other factors[3–7]. Mean SSTs have been forecast to rise above the 1998 values in a few decades[2,3]; however, forecast SSTs rarely flow seamlessly from historical data, or may show erroneous seasonal oscillations, precluding an accurate prediction of when lethal SSTs will recur. Differential acclimation by corals in different places complicates this further[3,7,8]. Here I scale forecast SSTs at 33 Indian Ocean sites where most shallow corals died in 1998 (ref. 1) to identify geographical patterns in the timing of probable repeat occurrences. Reefs located 10–15° south will be affected every 5 years by 2010–2025. North and south from this, dates recede in a pattern not directly related to present SSTs; paradoxically, some of the warmest sites may be affected last. Temperatures lethal to corals vary in this region by 6 °C, and acclimation of a modest 2 °C by corals could prolong their survival by nearly 100 years.

Timing of recovery from the 1998 massive coral mortality on Indian Ocean reefs (refs 1, 2, 6 and Fig. 1) and how frequently rising SSTs will cause repeat mortalities are issues of practical urgency for many countries because of the high value of reefs to shoreline protection, biodiversity, protein supply and tourism[6,9,10]. Raw, modelled SSTs cross supposed thresholds of coral bleaching in a few decades[2], but scaling problems in forecast data, coral acclimation[3,7,8] and different absolute SSTs and rates of SST rise vary markedly between sites, which greatly affects estimates of when rising temperatures will reach values that proved lethal before. Exact dates remain unattainable, but a probability approach proves very revealing in terms of both timing and geographical pattern. Using the Indian Ocean, whose reefs were worst affected in the warm SSTs of 1998, I have 'blended' forecast SSTs seamlessly onto historical SST data, with appropriately scaled forecast seasonal cycles, for 33 sites.

Historical SST data from 1871–1999 from the HadISST1 data set[11,12] were combined with surface ('skin') temperature from 1950–2099 from the HadCM3 model for each site; the latter equates with SST (see http://www.cru.uea.ac.uk/cru/info/modelcc/). Both series are monthly; HadISST1 cells are 1° latitude and longitude, whereas the HadCM3 cells used are 2.5 × 3.75° (http://www.cru.uea.ac.uk/cru/info/modelcc/). HadISST1 comprises the latest historical data[11] and HadCM3 is the most recent 'coupled' model from the Hadley

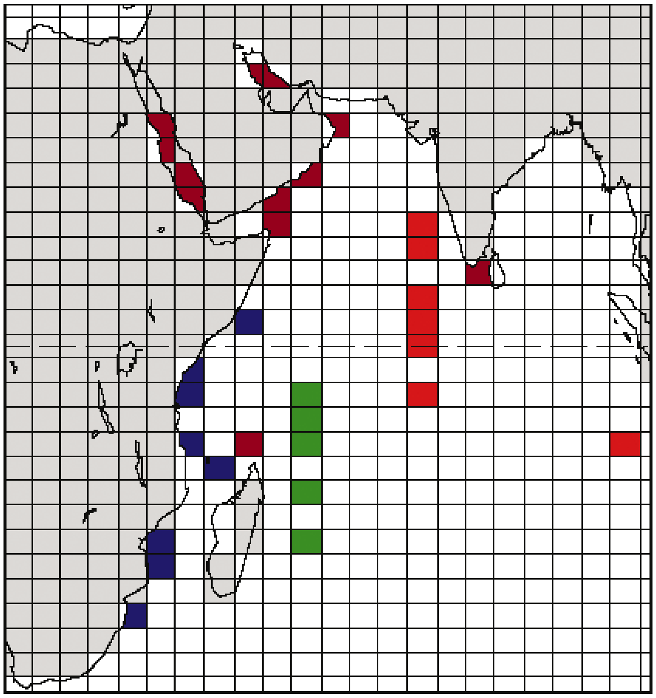

Figure 1 Coral reef sites in the western Indian Ocean where 1998 SSTs caused mass coral mortality. The grid comprises HadCM3 cells. Blue, green and red filled cells show the transects studied; colours match the curves in Fig. 4. Brown shows additional sites examined (Arabian region, Aldabra and Sri Lanka) that do not form coherent transects (Sri Lanka is located near the central chain of atolls but is a 'high island' with reefs of very different character; Cocos Keeling, the eastern-most site, is a typical atoll and is included in the central atolls group.)

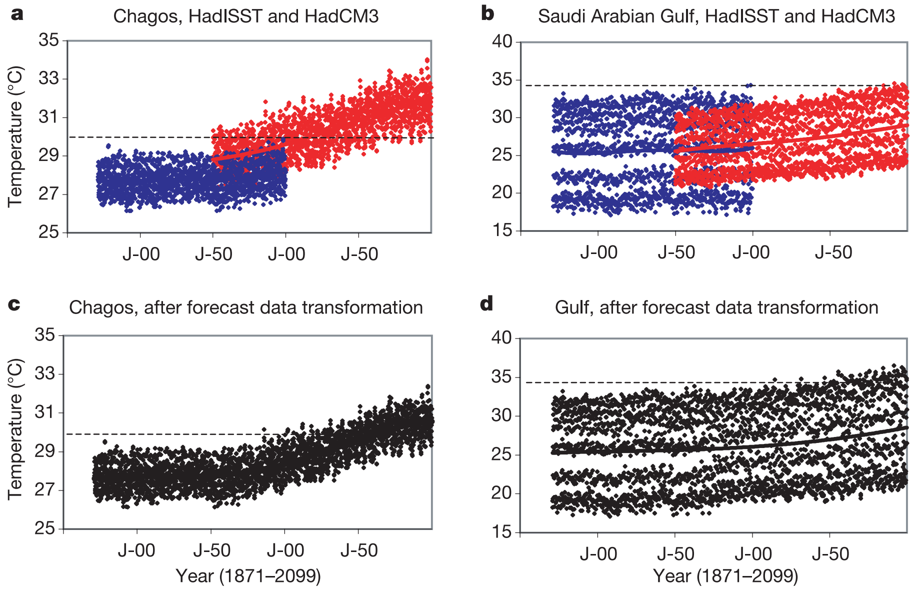

Figure 2 Historical and forecast SST data from two sites before and after the transformations. Historical data (HadISST1) are blue, and forecast data (HadCM3, IS92a) are red. Black points are data after transformation. **a**, **c**, Typical oceanic site of Chagos archipelago. **b**, **d**, Extreme continental site of Saudi Arabian Gulf. Dotted horizontal lines indicate SST values that killed corals in 1998. Curves of best fit are Excel's fourth-order polynomials.

Centre[13]. Other data sets can be substituted with minimal changes to the pattern described (Supplementary Information). With regard to warming schemes, more than 40 exist today; the one chosen is the thoroughly tested IS92a scheme[14], which follows a median path[13,14] and has been most used for inter-comparisons (Supplementary Information).

'Raw' SST data require transformation before use (Fig. 2). In typical oceanic atolls (Chagos), historical and forecast series are discontinuous by more than 1.5 °C. In an exceptionally variable site (Saudi Arabian Gulf), measured SST amplitude is the highest known for coral reefs (15 °C) but its forecast SST series shows an erroneously small seasonality, which would mislead because it is the annual high SST that causes mortality[15].

From each SST series (Methods), the probability of repeat critical SSTs can be determined. Four sites illustrate this (Fig. 3): those noted above plus those with the fastest and slowest rates of rise among these 33 sites. These curves integrate: the absolute SST at a site, its rate of rise, and the temperature that was lethal to more than 90% of the shallow corals there in 1998, which is a function of acclimation. The coral species are all from the same western Indian Ocean subset of fauna, with relatively few endemic exceptions[16,17].

Mortality in 1998 was triggered by SST rises lasting as short as the warmest month, although warming lasted 3 months in many areas[1,2,18–22]. As it is not yet known exactly how much warming triggers bleaching leading to mortality (or for how long), probability of recurrence curves are computed with warmest month, warmest 3 months and averaged warmest quarter. To compare these across sites, a uniform 'extinction date' is required. Although almost any point will suffice to show the geographical pattern, the date chosen is the year when there is a 0.2 probability of the warmest month (or warmest 3 months or averaged warmest quarter) hitting the 1998 value. The value 0.2 is ecologically fairly realistic: most corals do not mature until 5 years old[2,23] and today, 5 years after the

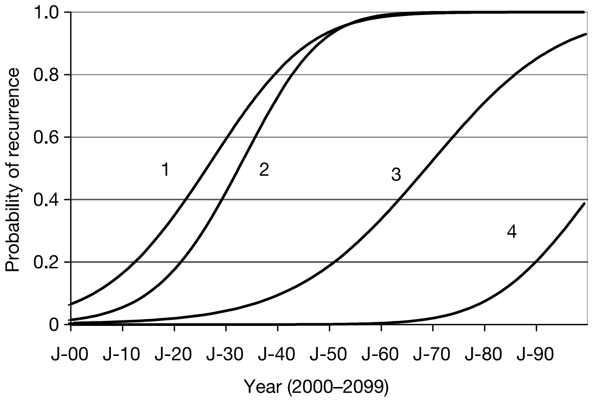

Figure 3 Probabilities of the warmest months of four sites reaching the lethal 1998 temperatures over time. Middle curves are sites used in Fig. 2; outer curves are two extremes. 1, Comores (African coast transect); 2, Chagos; 3, Saudi Gulf; 4, Minicoy, North Lakshadweep. The warmest month was March in Comoros and Chagos, May in North Lakshadweep, and September in Saudi Arabian Gulf.

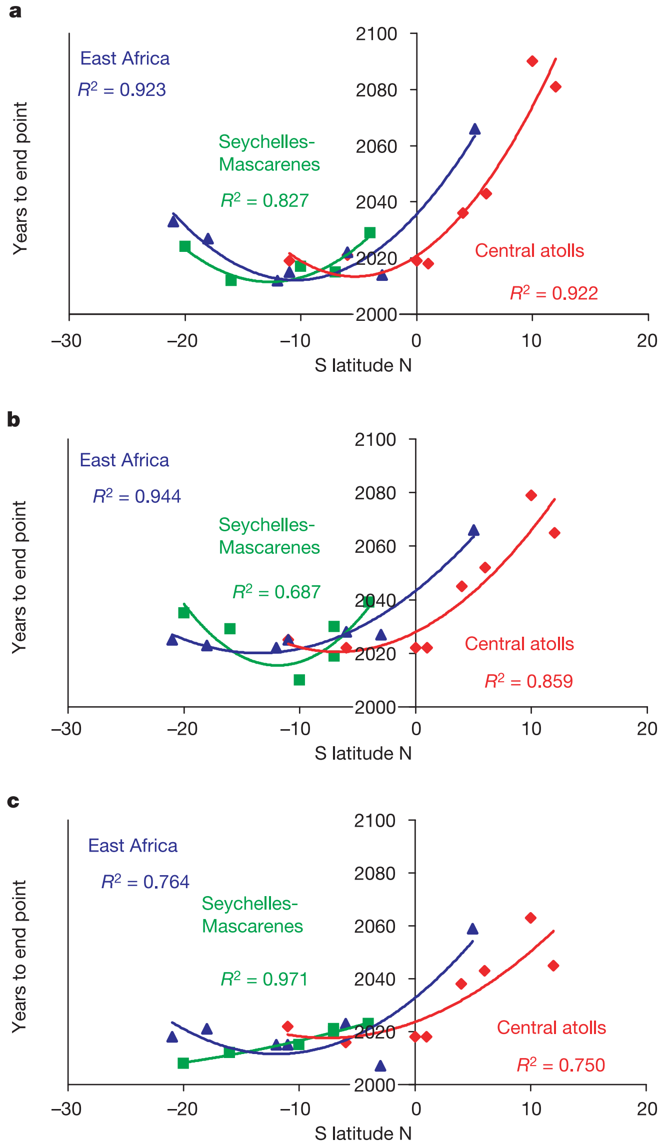

Figure 4 'Extinction dates' plotted for coral reef sites on the three transects, showing the date when a probability of 0.2 is reached. All curves are significant fits. **a**, Warmest month. **b**, Warmest 3 months. **c**, Warmest quarter. Colours match sites of Fig. 1. If the eastern Cocos Keeling atoll is removed from the central atoll transect, R^2 values for that transect remain almost unchanged (0.921, 0.868 and 0.780, respectively). If the continental reefs of Sri Lanka are added to that transect, R^2 values drop slightly (0.742, 0.833 and 0.747, respectively) but are still significant ($P < 0.01$).

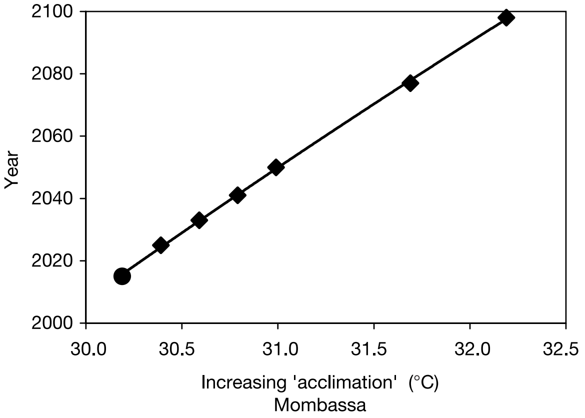

Figure 5 Recession of time to extinction date with imagined acclimation of corals by up to 2 °C with Kenya as the example. Dot is the existing situation, diamonds are the extinction date given coral 'acclimation'.

1998 event, most of these sites have recovered only marginally[19], with coral cover rising in shallow water from 1–2% immediately after 1998 to about 3–5% today, as compared with pre-1998 values of 40–75% (refs 19–22).

Whether warmest month, warmest 3-month period or averaged warmest quarter values are used, earliest vulnerability will occur between 10–15° south (Fig. 4) between 2010 and 2025 along all three north–south transects. These 'extinction dates' recede southwards, but also recede northwards, initially towards the equator. The Arabian sites have a confused pattern owing partly to a "pseudo-high latitude effect"[24] caused by cold summer upwelling in the Arabian Sea, such that some sites with highest temperatures have the most distant extinction dates; in others, upwelling precluded determination of the 'extinction date' (Supplementary Information). Many Arabian corals annually survive temperatures that killed the same species elsewhere in 1998 (refs 15, 19, 20). The northern Red Sea remains relatively unaffected but, even with their marked temperature acclimation, most corals in the Arabian Gulf were killed by the 1998 peak SSTs. The fact that most sites between 0° and 15° south will have a 1 in 5 probability annually of suffering a month as warm as that of 1998 within 10–15 years means that several of the world's poorest countries, for which reefs provide essential resources[6,9,10], will be affected soonest.

A modest acclimation or adaptation by corals[7,8] would greatly prolong time before their 'extinction date'. In 1998, lethal SSTs varied by 5 °C (from <29 °C to >34 °C) depending on location. By raising the SST presumed to be lethal at a site by 2 °C, nearly a century will be gained (Fig. 5). A value of 2 °C seems modest compared with that already achieved by today's Arabian corals[15,17], but the latter had millennia to acclimate. In these 33 sites today, total coral cover has improved little since 1998 (refs 18–20). The few decades before probable recurrence of lethal SST values may not be sufficient for recovery to become well established.

Diverse physiological and pathological factors are triggered by a rise in SST. Most act with, or are triggered by, temperature[7]. Some physical factors such as increased cloudiness[4] and water exchange[5] oppose these effects. SST should not be taken as the only important factor, although it is at worst a quantitative, measurable surrogate. ☐

Methods

Scaling of forecast data series

SSTs forecast from climate models rarely flow seamlessly from historical series, and errors in forecast seasonal amplitudes further prevent accurate estimation of when lethal mortalities might recur. The first transformation simply adjusts each forecast data series by the mean difference in values in the overlapping data between 1950 and 1999 ($n = 600$ months).

The second transformation scaled the seasonal amplitude of each forecast series to match that of each site's historical data. Fourth-order polynomial fits were computed for each historical series. Fourth order was chosen by extensive trial and error; orders up to fourth significantly increased R^2, whereas higher orders added no significant further improvement. Predicted values were subtracted from their corresponding monthly data points to obtain series of residuals. This was repeated for forecast data at each site. Correlations between residuals of the historical and forecast SSTs at each site in overlapping years (1950–1999) are always highly significant; in the examples plotted, (Fig. 2), $r = 0.973$ for the Gulf and $r = 0.762$ for Chagos ($n = 600$).

By using the 'normdist' function of Excel (Microsoft), residuals of forecast series were expressed as standard deviations. By substituting the standard deviation of the historical data residuals in place of that of the forecast data, Excel's 'norminv' function was then used to compute forecast temperature residuals whose annual oscillation matches in magnitude that of the historical series. Adding these scaled residuals back to the polynomial curves gives, for every site, an SST series (1871–2099) with no disjunction and, where they overlap, the same seasonal amplitude.

Standard deviations of HadISST1 residuals are stable with time[11]. HadCM3 residuals increase in amplitude by 3–25% with time, reflecting the climate model's increasing uncertainty into the future, and this is carried through in the transformed series. Other historical SST series could be substituted; the changes to the pattern are minor to negligible (Supplementary Information).

Computing probabilities of recurrence

Subsets of data were extracted for warmest months, three warmest months and averaged warmest quarters of each year. Residuals of all but one (Alphonse atoll) warmest month series have normal distributions (Kolmogorov–Smirnov tests). Warmest quarters' residuals are also normally distributed in all sites except one (granitic Seychelles). As time proceeds, the difference between the lethal 1998 SST value (also expressed as a residual) and the normally distributed population of SSTs decreases. For each month, '1 − normdist' determines the probability that each site's lethal temperature is part of the site's population of temperatures. This yields probability curves of repeat recurrences of the peak temperature of 1998.

In the warmest 3-month data sets, residuals in only half of the sites have normal distributions (they lack extended 'tails'). For these, 'bootstrap tests' were used instead of the normdist function to compute probability; probability was the number of residuals in the whole data set with a value greater than the test value, divided by the total number. Curves almost exactly match those obtained by the normdist method. This test was also used for the north Seychelles site for the quarterly series to extend that transect northwards; the test differed by less than 1 year from that obtained with the normdist function at that site.

'Lethal' SSTs and timing

Peak SSTs ranged from February in the south to September in the northwest. For 27 sites, the warmest quarter was the peak month with the preceding and the following months. For the other six sites, it was the peak month with the two preceding months. For the warmest month and 3-month tests, the test SST value was the warmest 1998 HadISST1 temperature. For the warmest quarter test, the average SST of the warmest 3 months was used. These temperatures were generally only less than 0.2 °C warmer than any earlier recorded temperatures at that site.

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Monkeys reject unequal pay

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During the evolution of cooperation it may have become critical for individuals to compare their own efforts and pay-offs with those of others. Negative reactions may occur when expectations are violated. One theory proposes that aversion to inequity can explain human cooperation within the bounds of the rational choice model[1], and may in fact be more inclusive than previous explanations[2–8]. Although there exists substantial cultural variation in its particulars, this 'sense of fairness' is probably a human universal[9,10] that has been shown to prevail in a wide variety of circumstances[11–13]. However, we are not the only cooperative animals[14], hence inequity aversion may not be uniquely human. Many highly cooperative nonhuman species seem guided by a set of expectations about the outcome of cooperation and the division of resources[15,16]. Here we demonstrate that a nonhuman primate, the brown capuchin monkey (*Cebus apella*), responds negatively to unequal reward distribution in exchanges with a human experimenter. Monkeys refused to participate if they witnessed a conspecific obtain a more attractive reward for equal effort, an effect amplified if the partner received such a reward without any effort at all. These reactions support an early evolutionary origin of inequity aversion.

In preliminary studies, two conditions were used: 'equality', in which two monkeys exchanged tokens with a human experimenter

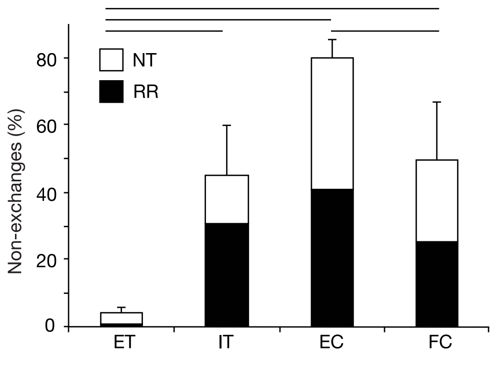

Figure 1 Mean percentage ± s.e.m. of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward; white bars (NT) represent those due to refusals to return the token. s.e.m. is for combined non-exchanges. Lines indicate significant differences between conditions (Tukey's multiple comparisons). ET, equality test; IT, inequality test; EC, effort control; FC, food control.