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Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia

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Abstract In April–May 1998, mass coral bleaching was observed in the lagoon of Rangiroa Atoll, Tuamotu Archipelago, French Polynesia. Six months later, the extent of bleaching-induced coral mortality was assessed at three sites. Corals in the fast-growing genus *Pocillopora* had experienced >99% mortality. Many large colonies of the slow-growing genus *Porites* (mean horizontal cross-sectional area 5.8 m²) had also died – a phenomenon not previously observed in French Polynesia and virtually unprecedented world-wide. At one site, 25% of colonies, or 44% of the pre-bleaching cover of living *Porites*, experienced whole-colony mortality. At the two other sites, recently dead *Porites* accounted for 41% and 82% of the pre-bleaching live cover. Mortality in *Porites*

was negatively correlated with depth between 1.5 and 5 m. Using a 50-year dataset of mean monthly sea surface temperature (SST), derived from ship- and satellite-borne instruments, we show that bleaching occurred during a period of exceptionally high summer SST. 1998 was the first year in which mean monthly SSTs exceeded the 1961–1990 upper 95% confidence limit (29.4°C) for a period of three consecutive months. We suggest that the sustained 3-month anomaly in local summer SST was a major cause of coral mortality, but do not discount the synergistic effect of solar radiation. Recovery of the size-frequency distribution of *Porites* colonies to pre-bleaching levels may take at least 100 years.

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Introduction

The 1997/1998 El Niño Southern Oscillation (ENSO) event is widely believed to have been the most severe in recorded history, provoking unprecedented levels of coral bleaching and subsequent mortality world-wide (International Society for Reef Studies 1998; Wilkinson 1998; Wilkinson et al. 1999). Coral bleaching refers to the paling of coral tissue brought about by loss of symbiotic dinoflagellate algae (zooxanthellae) and/or their pigments (Glynn 1993; Brown 1997). Bleaching has been observed in response to a variety of physical phenomena, including extremes of temperature, irradiance and salinity (see reviews: Brown 1997; Hoegh-Guldberg 1999). The precise combination of causative agents involved in large-scale bleaching of corals in 1998 is unclear. The most widely accepted view is that bleaching was caused by exceptionally high sea temperature acting synergistically with solar radiation (International Society for Reef Studies 1998; Wilkinson 1998). This hypothesis is favoured because most bleaching episodes have occurred in summer, during calm sea conditions, near to the time when solar radiation was presumed to be maximal (see Glynn 1993).

Wilkinson (1998) has summarised accounts of coral bleaching globally and notes that ca. 80% of reports are

anecdotal and possibly exaggerated by the stark appearance of bleached corals. Here, we provide a quantitative estimate of coral mortality measured 6 months after a mass bleaching event in the lagoon of Rangiroa Atoll, the second largest atoll in the world. To make a cursory examination of causal processes, we utilise a 50 year record of sea surface temperature (SST). The potential recovery of coral community structure to pre-bleaching levels is discussed. We conclude that the high level of mortality in colonies of *Porites*, which is usually resistant to bleaching-induced mortality, are unprecedented in French Polynesia and possibly globally.

Materials and methods

Study sites

Widespread coral bleaching was observed in the lagoon of Rangiroa Atoll (15°0'4.3"S; 147°52'51.8"W), situated approximately 350 km northeast of Moorea, during April and May of 1998. Six months later, three reefs, spaced 10s of kilometres apart, were surveyed using 1 m² quadrats (Fig. 1), primarily to provide ground-training information for a remote sensing survey. One of the reefs, Tivaru, was selected to obtain specific estimates of the mortality of large coral colonies. We do not claim that the three reefs were statistically representative of the atoll, although we believe that they provided informative snapshots of coral mortality in different physical environments. One reef (named after the nearby Motu Nuhi) was located in the north of the atoll, on the western side of the main reef pass, Tiputa. It therefore experienced relatively high tidally driven water flow originating alternately from the open ocean and the interior of the atoll. The other two reefs, Motu Tivaru and Motu Tetaa, were located in sheltered parts of the western and southern sectors of the atoll, respectively. All reefs were located within ca. 1–2 km of the atoll rim, in water of 1–5 m depth, and they each measured ca. 1 km in length.

Benthic cover

Benthic cover was estimated using a 1 m² quadrat, subdivided into 0.2×0.2 m squares to provide a maximum spatial resolution of measurement of 0.04 m². A total of 38 quadrats were sampled in

randomly selected locations on the reef at Motu Tetaa. On the other two reefs, quadrats were deployed in 25 m² blocks (5×5 m squares); ten replicate blocks in randomly chosen locations were surveyed at Motu Nuhi; seven were surveyed at Motu Tivaru. To estimate benthic cover on each reef using the same sample unit, 1 m² square areas were subsampled at random within each dataset, provided that they did not occur adjacent to one another. A total of 130 quadrats (1 m²) were sampled at Motu Nuhi; 91 quadrats were sampled at Motu Tivaru.

The surfaces of massive coral colonies tend to comprise mosaics of living tissue and dead skeletal patches colonised by algae (partial colony mortality *sensu* Hughes and Jackson 1985). We assigned the label “live coral” when living tissue exceeded ca. 80% and “partially dead” when living coral cover was < 80% (although the cover of living tissue rarely fell below 30% on such colonies). Following mortality, the calcareous corallite structure of the coral polyp becomes progressively obscured by algal colonisation and bioerosion of the underlying skeletal carbonate by herbivores (Bak 1994). The terms “recently dead” and “old dead” (see Ginsburg et al. 1998) were adopted to categorise coral mortality states. To summarise, coral categories were:

- live (≥80% living cover),
- partially dead,
- recently dead (corallite structure visible, usually colonised by filamentous algae) and
- old dead (corallite structure absent, grazing scars of herbivores often visible).

These definitions were applied to each 0.04 m² of reef when estimating coral cover. Measurements of the greatest and least diameters of 61 massive *Porites* colonies selected at random from five, 6-m-wide belt transects, were made at Motu Tivaru to determine if there was a relationship between colony size and mortality state. In this survey the designation of coral category was scaled to entire colonies.

Effect of depth on recent *Porites* mortality

The effect of depth on recent mortality in massive *Porites* colonies was examined by pooling all data gathered at Motu Nuhi and Motu Tivaru (i.e. seventeen 5×5 m blocks). The severity of mortality was estimated as a proportion of the live coral cover prior to the mortality event (i.e. the cover of recently dead coral divided by the combined cover of recently dead and live *Porites*). Following Anderson–Darling tests for normality (Minitab 1997), the severity of *Porites* mortality was examined as a function of depth.

Fig. 1 Rangiroa Atoll (Tuamotu Archipelago), French Polynesia showing the locations of three study sites. The three sites represent ca. 1–3% of the entire lagoon area in the 1–5 m depth range

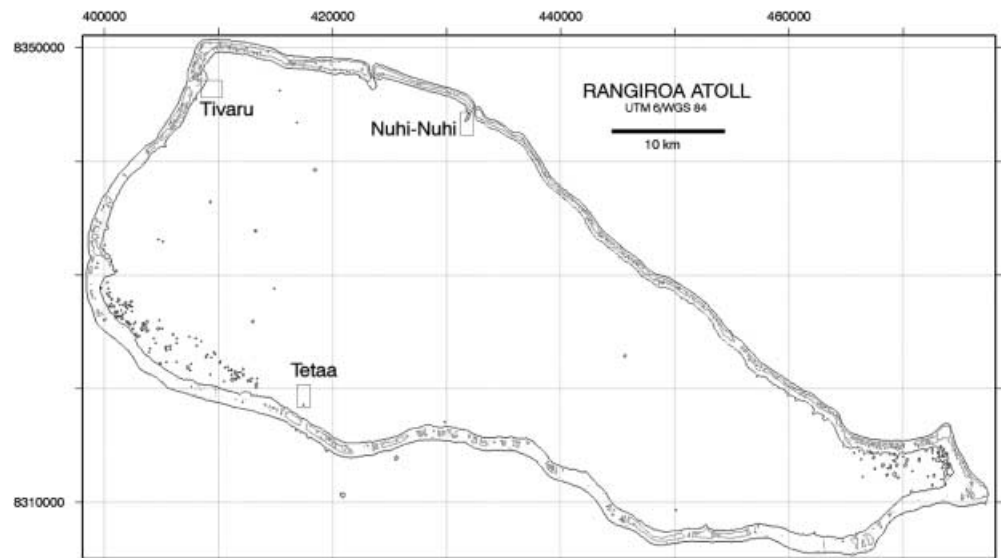
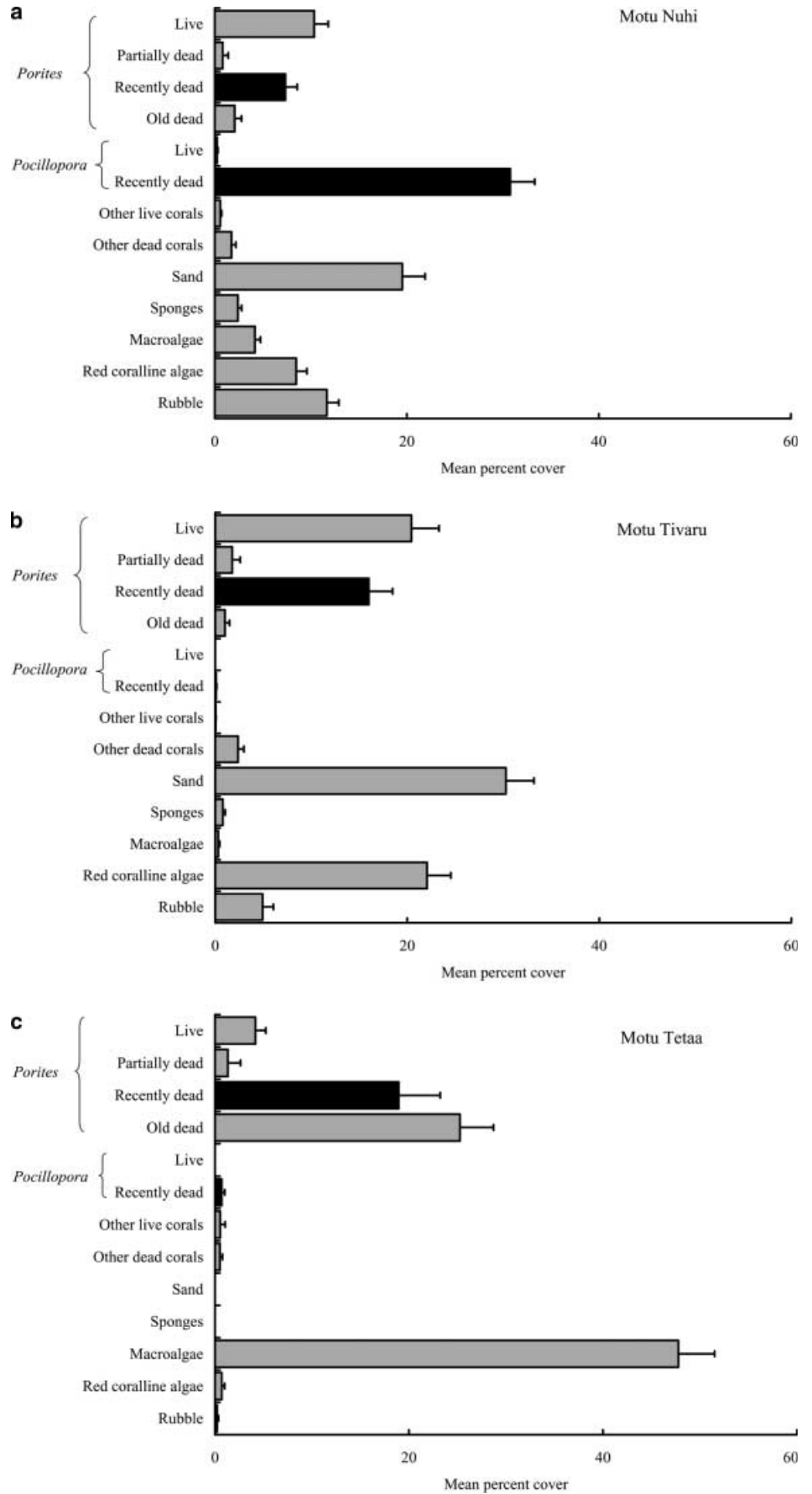


Fig. 2a–c Benthic community structure measured ca. 6 months after the 1998 bleaching event near Motu Nuhi (a), Motu Tivaru (b) and Motu Tetaa (c). Error bars represent standard error of the mean



Sea surface temperature (SST) records

The Global sea-Ice and SST dataset version 2.3b (GISST2.3b) for 1° latitude×longitude areas was used to examine the 1998 warming anomaly at Rangiroa. It was provided by courtesy of the UK Meteorological Office's Hadley Centre for Climate Prediction and Research. It uses an empirical orthogonal function to interpolate data-voids and provide global coverage (Rayner et al. 1996; Smith et al. 1996). Since 1982, a blend of bias-corrected AVHRR (Advanced Very High Resolution Radiometer) satellite-derived SST data and in situ data has been provided, which requires little interpolation (Parker et al. 1995; Rayner et al. 1996). The bias-correction adjusts for differences between oceanic skin temperature as measured by the satellite and in situ bulk sea surface temperature (Reynolds 1988).

Results

The coral community at Motu Nuhi was dominated by *Pocillopora eydouxi* in shallow water (1–3 m) and massive *Porites* spp. in deeper (3–5 m) water. Virtually all (>99%) of the *Pocillopora* had died recently, leaving large tracts of dead reef (Fig. 2). Old dead *Pocillopora* was not distinguishable as a separate category as it had been heavily bioeroded or colonised by algae. *Pocillopora* was rarely encountered at the sheltered reef sites although, where present, it had also died recently (e.g. Motu Tetaa; Fig. 2).

Whilst mortality was more severe in *Pocillopora* than in *Porites*, the extent of *Porites* mortality was unprecedented in French Polynesia. Twenty-five percent of all previously living (or partially living) *Porites* colonies died completely at Motu Tivaru. Moreover, the average horizontal cross-sectional area of these corals was 5.8 m² (± 1.5 SE), indicating that they had been growing for at least 200 years prior to 1998, assuming an average linear growth increment of ca. 1 cm year⁻¹ (Isdale 1983). The degree of recent mortality in *Porites* (expressed as percent of area of living coral dying subsequent to bleaching) was similar at Motu Nuhi (41%)

and Motu Tivaru (44%), but considerably higher at Motu Tetaa (82%). The incidence of partial mortality was low (<2%) at all sites (Fig. 2). *Porites* mortality, although highly variable, was negatively correlated with depth (Fig. 3, $r = -0.48$, $P < 0.05$).

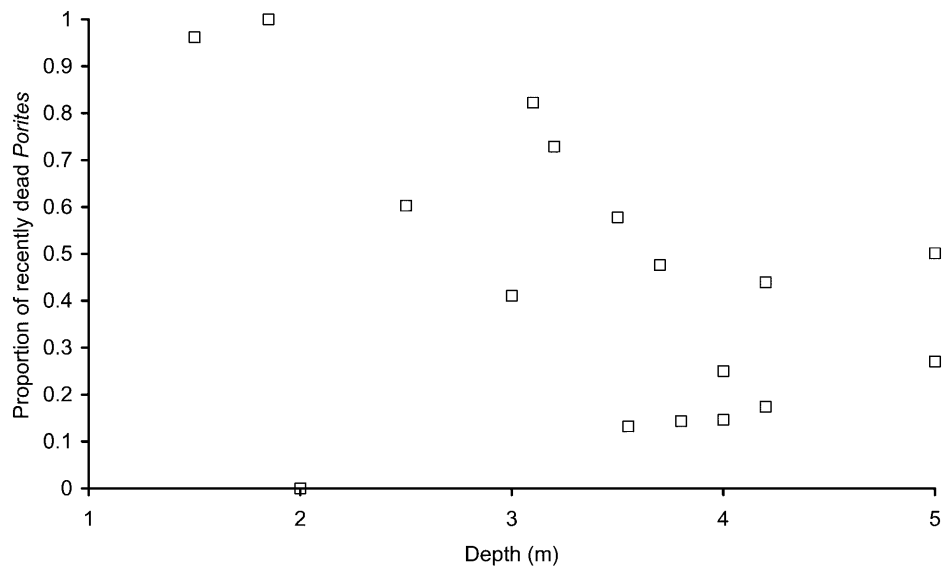
Sea surface temperature during March, generally the warmest month of the year, averaged 28.8°C between 1961 and 1990 (Fig. 4). In 1998, SST exceeded and remained above the upper 95% confidence limit of the mean temperature for March for a period of 3 months. Such a prolonged excursion above the upper confidence limit had not been previously recorded (Fig. 5).

Discussion

The rate of disappearance of corallite structure from a dead coral is a function of the rate of erosion and the rate of colonisation of the skeletal surface by other organisms, initially algae. Although it is impossible to discern, posthumously, the exact timing and cause of coral mortality, it appears possible to distinguish recently dead corals (ca. 6 months) from old dead corals on the basis of their physical appearance (Clark et al. 2000). Much of the dead coral surveyed at Rangiroa Atoll possessed sufficient corallite definition for us to conclude that large-scale mortality followed the bleaching event that occurred earlier in the year.

This is the first bleaching study at Rangiroa Atoll, so the causes of bleaching cannot be examined by hind-casting earlier events. However, the sustained 3 month period of SST anomalies was unprecedented in at least 50 years, and therefore SST seems the most likely factor to have caused the bleaching and subsequent mortality. Many other studies have also linked elevated SST to the incidence of bleaching (e.g. Goreau and Hayes 1994; Hoegh-Guldberg and Salvat 1995; Davies et al. 1996; Jones et al. 1998; Winter et al. 1998; Wilkinson et al.

Fig. 3 Depth versus the severity of bleaching-induced mortality in *Porites* spp. at Motu Nuhi and Motu Tivaru. Severity was measured as the cover of recently dead coral divided by the sum of recently dead and living coral cover. Each sample represents a 5×5 m quadrat



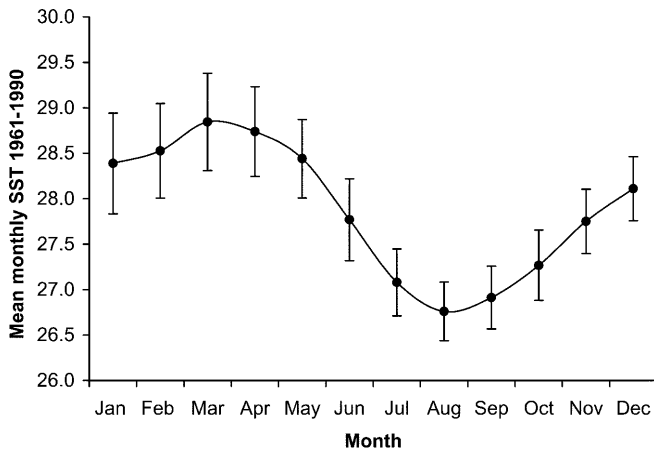


Fig. 4 Mean monthly sea surface temperature (*SST*) in the Rangiroa area (14–16°S; 147–149°W) between 1961 and 1990. Error bars indicate 95% confidence levels

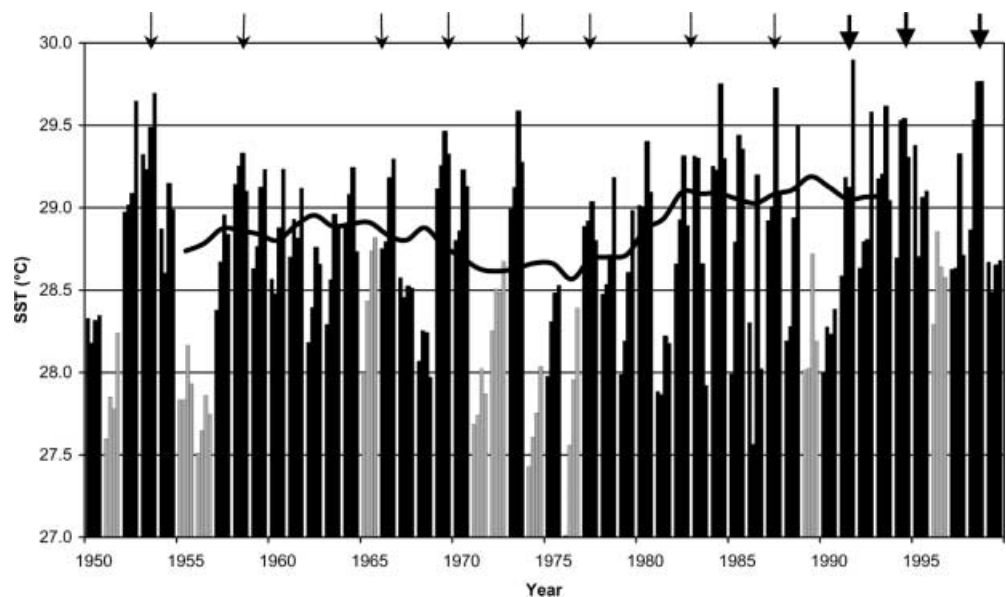
1999; Goreau et al. 2000). However, physiological studies suggest that radiative stress is a key causal factor in bleaching, and is exacerbated under conditions of high temperature (Lesser et al. 1990; Fitt and Warner 1995; Warner et al. 1996; Brown 1997; Iglesias-Prieto 1997; Lesser 1997; Jones et al. 1998; Hoegh-Guldberg 1999). Reduced efficiency of utilising photosynthetic energy (Osmond 1994) occurs when the zooxanthellar photosystem is saturated with photosynthetically active radiation. Unless excess excitation energy is dissipated (e.g. by the xanthophyll cycle; Brown et al. 1999), photo energy is directed to the creation of harmful (e.g. oxygen) free radicals, which disrupt photosystems and cause bleaching (Lesser et al. 1990; Lesser 1997; Brown 1997; Jones et al. 1998). Solar irradiance measurements were unavailable for Rangiroa, and therefore we do not discount the importance of solar radiation in explaining

mass bleaching at this site. (Note: on-going research in the Society Islands suggests that solar radiation might affect the occurrence of mass bleaching; the results will be published elsewhere.) Indeed, solar radiation has been invoked to explain depth-related patterns of bleaching or mortality elsewhere (e.g. Harriott 1985), and it is feasible that the inverse depth–mortality relationship observed for *Porites* resulted partly from exponential attenuation of solar radiation with increasing depth. However, depth-related patterns of mortality might also result from gradients of thermal stress or zonation in the physiological tolerance of the corals and/or their zooxanthellate symbionts (Rowan et al. 1997; Brown et al. 1999, 2000).

Smaller, faster growing coral species in the genera *Acropora* and *Pocillopora* have been widely reported to suffer greater bleaching-induced mortality than larger, long-lived colonies such as *Porites* (Glynn 1984; Gleason 1993; Salvat 1993; Hoegh-Guldberg and Salvat 1995; present study). The greater resilience to bleaching of large colonies of *Porites* has been attributed to their slow metabolic and growth rates (Glynn 1993), which render them less vulnerable to photosynthetic or translocatory dysfunction. Further, Hoegh-Guldberg (1999) suggested that the tissues of *Porites* spp. are better shaded from solar irradiance because they are located deeper within the skeleton than tissues of *Acropora* spp. or *Pocillopora* spp. However, an important observation in the present study was the 25% loss of *Porites* colonies and 40–80% loss of *Porites* coral cover, much of which involved large colonies (up to 8 m diameter) which were hundreds of years old (Isdale 1983). Such severe mortality in *Porites* is unique for French Polynesia, and possibly unprecedented globally throughout the 1998 bleaching event (Wilkinson 1998).

To make a crude estimate of the potential for recovery of the size-distribution of *Porites* to its pre-bleaching

Fig. 5 Mean monthly sea surface temperature (*SST*) in the Rangiroa area between 1950 and 1998 for January, February, March and April. Lightly shaded columns represent La Niña years, arrows indicate El Niño years, and thick arrows denote El Niño years in which mass bleaching was reported in French Polynesia. Continuous line across years denotes 11 year running mean of *SST*



state, it is instructive to examine the model of Done (1988), which simulated the recovery of large *Porites* colonies (> 3 m diameter) on the Great Barrier Reef after a quarter were killed outright by the crown-of-thorns starfish, *Acanthaster planci*. Most reefs would take at least 100 years to recover their previous abundance of large corals assuming that favourable conditions predominated, no future acute disturbance occurred and that dead coral skeletons were re-colonised rather than new reef structure developed. If disturbances continued at 10–30 year intervals, all large colonies would be lost unless background mortality was low and recruitment of *Porites* was high. Such model simulations predict a bleak future for the coral communities in the lagoon of Rangiroa Atoll in the light of: (1) the recent apparent increase in frequency and magnitude of bleaching phenomena; (2) the fact that two out of the three years in which SST anomalies rose above the long-term 95% confidence limit for mean March temperature for 2 months or longer in French Polynesia belong to the present decade; and (3) the predicted future increase in strength and frequency of ENSO events in the tropical Pacific (Timmermann et al. 1999). It appears that the fate of these reefs will depend on their ability to increase tolerance of environmental stress or select for more bleaching-resistant strains of corals and/or zooxanthellae.

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