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Mass mortality events in atoll lagoons: environmental control and increased future vulnerability

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Abstract

Coral reefs and lagoons worldwide are vulnerable environments. However, specific geomorphological reef types (fringing, barrier, atoll, bank for the main ones) can be vulnerable to specific disturbances that will not affect most other reefs. This has implications for local management and science priorities. Several geomorphologically closed atolls of the Pacific Ocean have experienced in recent decades mass benthic and pelagic lagoonal life mortalities, likely triggered by unusually calm weather conditions lasting for several weeks. These events, although poorly known, reported, and characterized, pose a major threat for resource sustainability. Based on a sample of eleven events on eight atolls from the central South Pacific occurring between 1993 and 2012, the conservative environmental thresholds required to trigger such events are identified using sea surface temperature, significant wave height and wind stress satellite data. Using these thresholds, spatial maps of potential risk are produced for the central South Pacific region, with the highest risk zone lying north of Tuamotu Archipelago. A regional climate model, which risk map compares well with observations over the recent period (r = 0.97), is then used to downscale the projected future climate. This allows us to estimate the potential change in risk by the end of the 21st century and highlights a relative risk increase of up to 60% for the eastern Tuamotu atolls. However, the small sample size used to train the analysis led to the identification of conservative thresholds that overestimated the observed risk. The results of this study suggest that long-term monitoring of the biophysical conditions of the lagoons at risk would enable more precise identification of the physical thresholds and better understanding of the biological processes involved in these rare, but consequential, mass mortality events.

Keywords: climate change, CMIP-3, CMIP-5, coral reef, dystrophy, Pacific Ocean, sea surface temperature, significant wave height, wind stress

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Introduction

Not all coral reef types are equally vulnerable to all disturbances. Weather and climate driven disturbances call for mitigation programs that must tailored for every configuration of reefs, levels of exposure and levels of vulnerability. In particular, atoll lagoons in the Pacific Ocean are unique reservoirs of biodiversity, with several shallow and intertidal habitats and communities found nowhere else on earth. Livelihood of many remote human populations on atolls have heavily relied on their protected lagoon waters before and after Europeans landed on atoll shores. Nowadays, isolated islanders in Polynesia, Micronesia and Melanesia still rely on lagoon resources for daily subsistence, while more accessible lagoons have been extensively transformed by tourism, commercial fishing, aquaculture and in some cases, by military activities such as nuclear weapons testing in the Marshall Islands and Tuamotu archipelagos.

Atolls are one of the end-members of a classification of coral reef ecosystems based on degree of closure (Hatcher, 1997). Although there is a wide range of closure between atolls (Andréfouët *et al.*, 2001a), they are seen as the most hydrodynamically closed reef systems, with limited exchanges between the inner lagoon and the outer oceanic system. The lagoon closure can be seen as a protection, against storms for instance, but high water residence time also increases the risk of water quality problems, invasions, shifts, mortalities and biodiversity loss. The main disturbances and threats to atoll lagoon ecosystems identified in the current literature encompass climate change related impacts (through warming, acidification and sea level

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rise), hurricanes, overfishing, human-induced pollution and shore modifications (Bell *et al.*, 2011). Less attention has been paid to dystrophic events in lagoons that have resulted in mass mortalities and wiped out benthic and pelagic lagoonal life within a few weeks, such as in Hikueru atoll (French Polynesia) in 1994 (Harris & Fichez, 1995; Adjeroud *et al.*, 2001) (see Figure S1 for location map of atolls). Andréfouët *et al.* (2013) reported in 2009 a 90% mortality of giant clams, which used to dominate the benthos at Tatakoto atoll (Figure S2). Recently, Hobbs (2012) reported another mass mortality of fishes and invertebrates in January 2012 in an Indian Ocean atoll. This was attributed to a combination of unusual weather and trapped coral spawn that likely led to hypoxia. As with major earthquakes and tsunamis in other areas, mass mortality events in atoll lagoons are few, but they can have tremendous consequences for local human communities. At first sight, these rare events appear to occur randomly since one atoll can be impacted while nearby atolls (less than a hundred kilometres away) are not. They also appear to be unpredictable, although some atolls appear to be more vulnerable than others.

These overlooked events in the hierarchy of threats to coral reef ecosystem are presumably weather-driven (Bell & Galzin, 1984; Adjeroud *et al.*, 2001; Hobbs, 2012). Mass mortalities of benthic organisms in other parts of the world, although poorly understood, have been also related to heat waves or other weather anomalies (Garrabou *et al.*, 2009; Micheli *et al.*, 2012; Pairaud *et al.*, 2014), disease (possibly caused by thermodependent pathogens) and perturbations in the food chain (e.g. Pernet *et al.*, 2014). Disease and food availability alone cannot explain mortality of sponges, mollusc and fishes as witnessed in atoll lagoons. Although the biophysical mechanisms in the water column responsible for these events remain unobserved and cannot be ascertained, the primary factors controlling the occurrences of the events are most likely related to hydroclimatic conditions around the atoll. Calm weather, especially during the summer season, results in less active water lagoon renewal. In the case of geomorphologically closed to semi-enclosed lagoons, low wave conditions hydrodynamically isolate the lagoon, and low wind speeds can shut down the wind-induced circulation, leading to stratification. This isolates subsurface waters from air-sea exchange and rapidly translates into an anoxic water body. Different forcing mechanisms acting alone or in conjunction have been discussed, including the timing between a long period of calm weather and the following occurrence of a high energy event that may release nutrients into the lagoon water column (Harris & Fichez, 1995), extreme surface water warming (Adessi, 2001), and development of phytoplankton blooms, toxic or not, that alter the planktonic food web (Harris & Fichez, 1995). These different mechanisms (dystrophy and warming), or suite of mechanisms, have been suggested to explain mortalities that could be general or partial, found only below a certain depth or at the surface. Unfortunately, to the best of our knowledge, no *in situ* measurements have been performed to sample in real time the physical and hydrobiological conditions before and during a mass mortality event.

Not all atolls are equally vulnerable. It seems that open atolls are less vulnerable than closed ones. 'Open' vs. 'closed' is a semiquantitative terminology that classifies atolls according to the potential degree of exchange between lagoonal and oceanic waters. Intrinsic static factors such as geomorphology (presence of passes, or shallow spillways, Figure S3) and extrinsic dynamic factors such as tides, wind and swell regimes control openness which is thus time dependent (Andréfouët *et al.*, 2001a,b; Dufour *et al.*, 2001). The most severe recently reported events have all occurred in atolls without passes (e.g. Hikueru, Harris & Fichez, 1995; Adjeroud *et al.*, 2001; and Tatakoto, Andréfouët *et al.*, 2013), although atolls with passes have also experienced moderate events, such as those in Ahe in 2012 and in Mataiva in 1980 (Bell & Galzin, 1984). In practice, any atoll can temporarily turn into a closed atoll if the wind and swell are very low, and if the lagoon flushing is not maintained. Generally, in the absence of swell, minimal flushing is at least provided by tidally driven flows across the rim to the lagoon (as in Eniwetok, Marshall Islands, Atkinson *et al.*, 1981).

Human populations on atolls generally react to a mortality event only after noticing a strong impact on food or economical resources, with large numbers of fishes washed onshore, migration of fish schools trying to leave the lagoon, molluscs (such as giant clams and pearl oysters) dying or strongly discoloured (sometimes smelly) waters. In fact, many events probably went unreported before the 1970s. The development of communications and travelling facilities allowed more reporting of these events, but most reports were vague. Nowadays, in lagoons hosting black pearl farming and where subsistence fishing is critical, mass mortality can seriously threaten the livelihoods of inhabitants, and consequently the economy of the country. The cost of these events can be measured by direct resource losses but also indirectly, when financial subsidies are needed to support remote islanders left without resources. These atoll-specific massive disturbances can impact livelihoods more rapidly and significantly than, for example, a coral-bleaching event.

We revisit here the physical oceanographic conditions around the time of eleven reported events in the last two decades to identify potential environmental thresholds and conditions preceding mass mortality events. We also investigate why events appear spatially limited, striking one atoll but not neighbouring ones. This study, therefore, aims at understanding the environmental conditions favouring high risk of mortality in atolls and providing foundation knowledge to initiate early warning systems and real-time scientific monitoring. Enhanced knowledge will also be useful for decision makers when taking development actions (e.g. aquaculture) that could be vulnerable to future mass mortality events, ruining years of investments (Andréfouët *et al.*, 2013). Therefore, we also provide a spatial estimate of the changes in mortality probability between the present day and future climate at the end of the 21st century.

Materials and methods

Study area

The study area is the south central Pacific Ocean between 135°W–165°W and 5°S–25°S, including the atolls of the Tuamotu Archipelago, Society Archipelago (both in French Polynesia), and Cook Islands (see Figure S1). This area encompasses eighty-five atolls with a central water body (true lagoon, not dry or uplifted), with a large diversity of degree of closure. Atoll morphologies were mapped using high-resolution Landsat satellite images at 30-m resolution (Andréfouët *et al.*, 2006, 2008). This area has been selected because atoll lagoons in French Polynesia and Cook Islands are geomorphologically less open, and renewal is not primarily driven by tides (Atkinson *et al.*, 1981; Kraines *et al.*, 1999; Callaghan *et al.*, 2006; Dumas *et al.*, 2012), compared to other atoll groups found in the Marshall Islands, Kiribati (Gilbert group) and Federate States of Micronesia, Further, there are no published reports of mass multi-taxa mortalities in these other atoll groups, except for corals during bleaching events (e.g. Obura & Mangubhai, 2011).

Identification of past events and selection of environmental data

Mortality events between 1993 and 2012 were compiled mostly from grey literature, including field trip reports from the local technical services. Occasional reports of discoloured waters before this period are too vague, even in their timing, to be considered. Even for the recent 22-year period, we could not establish whether all the events that have occurred have been identified. Thus, 'false negative', or unreported occurrence of mortality, cannot be ruled out. Eleven unequivocal events occurring on eight different atolls (see Figure S1 for their location), likely displaying different rates of mortality, were identified (Table 1). Most of these atolls have their hydrodynamic functional apertures on the south rims.

Table 1 List of events identified in the 1993–2012 time period. The column 'Mortality' indicates for which biological group mortalities have been reported, but other groups could also have been impacted, and not been reported

Atoll	Date of event	Mortality
Hikueru	April 1994	Fish and benthos
Manihi	April 1994	Farmed oysters
Manihi	February 1997	Farmed oysters
Manihi	March 1998	Farmed oysters
Takapoto	March 1998	Benthos, farmed oysters
Takaroa	December 2000	Farmed oysters
Takaroa	January 2001	Farmed oysters
Fangatau	February 2004	Giant clams
Tatakoto	February 2009	Giant clams
Ahe	May 2012	Farmed oysters
Manihiki	February 2012	Farmed oysters

The period of investigation was also limited to the last 22 years, when both satellite and model data were available (Figure S4). Wind stress data between 1993 and 1999 were obtained from the European Remote Sensing ERS mission at weekly resolution (http://podaac.jpl.nasa.gov/dataset/ERS-2_IFREMER_L3_OW_MEAN_WIND_FIELDS). Daily wind data were then provided by the NASA Quickscat mission (http://oceanwatch.pifsc.noaa.gov) from 2000 to 2009 and by the NOAA Advanced Scatterometer (ASCAT) mission (http://coastwatch.pfeg.noaa.gov/erddap/gridap/) from 2010 onwards. For consistency, all wind data were resampled at a ¼° resolution, and weekly averaged for the entire 1993–2012 period. Daily sea surface temperature (SST) at ¼° resolution between 1993 and 2012 were obtained from the Advanced Very High Resolution Radiometer (AVHRR Pathfinder V4.1; ftp://podaac-ftp.jpl.nasa.gov/allData/ghrsst/data/L4/GLOB/NCDC/AVHRR_OI/). Ocean SST were used as proxies of lagoon surface temperature, which cannot be measured directly by satellite given the small size of some lagoons. Finally, the WAVEWATCH III model simulation run by IFREMER (ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/wavewatch3/HINDCAST/GLOBAL/; Rascle & Ardhuin, 2013) provided daily significant wave height (SWH) data at ½° resolution over the period of study. These data were remapped at ¼° and 7-day resolution.

Statistical analysis

Reports on mortality events often describe the final stages of the events, when fish are washed onshore and waters strongly discoloured. This coincides with the terminal stage of the process, but not to its initiation and development phase, for which the timing cannot be ascertained. Because of this uncertainty, it is not possible to set a specific time-lag to identify environmental anomalies that could have led to the mortality event. Examination of SST, wind stress and SWH time-series at several lags before the reported date (e.g. 3-days, 1 week, 2 weeks, 1 month) of the 11 reported events did not reveal any obvious anomalies that could help precisely identify event occurrences. We thus used a multivariate statistical approach to identify the conditions that could lead to events. For a one-degree latitude/longitude window around each atoll (Table 1), we computed weekly time-series of SST, wind stress and SWH from 1993 to 2012. Then, for each reported mortality event, we focused on a one-year time frame for each event (from 26 weeks before to 26 weeks after the event) to limit the data set used for the clustering analysis described below. This resulted in 548 week-long intervals of environmental data for 11 events and eight atolls. This is a 548 and not a 572 week-long dataset (11 events multiplied by 52 weeks), due to the short time difference between several events, which overlapped and were therefore considered only once. Finally, to allow enough time for the development phase of the event and given the uncertainty on the exact timing of the event, the 5 weeks before each reported event were flagged as risk periods. Since we had identified 11 events, we thus ended up with a total of 55 weeks of risk among the 548 weeks considered in our dataset.

First, to assess if the 55 risk weeks were characterized by specific environmental conditions, the 548 weeks were clustered based on their SST, SWH and wind stress values using hierarchical clustering (Ward distance and average aggregation, using the 'Cluster' package in the R programming environment). Second, a decision tree was applied to the 548 weeks of SST, SWH and wind stress values to identify hierarchical thresholds that discriminated the identified clusters. Finally, the occurrence frequency based on these thresholds was mapped over our study region over the 1993–2012 period. Both single factor frequency (e.g. occurrence of only the SST threshold) and triple-factor frequencies (simultaneous occurrences of SST, SWH and wind stress thresholds) were computed.

Autocorrelation of environmental factors

Most events were apparently very localized, affecting one atoll but not its neighbours, even when they are geomorphologically similar. For instance while severe mortalities occurred in Hikueru in 1994, no mortalities were reported in nearby and geomorphologically similar atolls (e.g. Nengo-Nengo, Hiti, ~180 km away from Hikueru). To understand why events seem so localized in space, we computed the daily spatial autocorrelation of SST, SWH and wind stress, starting 5 weeks before each event. The decrease in this autocorrelation in space illustrates the spatial extent of the environmental conditions observed at the focal atoll. Thus, autocorrelation helps to identify if an impacted atoll had very specific environmental conditions not found in nearby atolls, for about a month before the event.

Modelling present and future risks with environmental threshold occurrences

On the basis of the frequency of occurrences of the environmental thresholds found above, we projected the level of mortality risks in a changing climate. A number of precautions are needed to conduct a meaningful analysis. First, recent predictions on future wave climate suggest very limited changes for our study area, with a SWH variation of <2% (Fig. 2b in Hemer *et al*., 2013). We therefore kept this term constant for modelling future occurrences. Second, to confidently assess the risk changes in the future, it is necessary to use a model able to correctly simulate recent environmental conditions. However, it is recognized that several global climate models used by the Intergovernmental Panel on Climate Change (IPCC) poorly reproduce present-day South Pacific climate (e.g. Brown *et al*., 2013). We therefore make use of a 1° regional atmospheric model configuration developed for the tropical Pacific (95°E–115°W, 42°S–25°N) that correctly reproduces the present-day climate conditions. This model is based on the regional atmospheric WRF (Weather Research Forecasting) 3.2 model and is described and validated in Jourdain *et al.* (2011) and Jullien *et al.* (2012). This model accurately reproduces the climate of the South Pacific over the 1979–1999 time period. The present climate simulation ('REF') was forced at its boundaries by the NCEP2 reanalyses over the 1979–1999 period (Kanamitsu *et al*., 2002). For consistency with the observations, the daily REF outputs were weekly averaged. However, to compute threshold co-occurrences, the concurrent period with wave data was limited to 1990–1999. Finally, currently available model and observational data only overlapped for a short 6-year period, between 1993 and 1999 (Figure S4). This period is used to assess the level of agreement between historical observations and model.

The same atmospheric model configuration was used for projections, and to provide dynamical downscaling of an ensemble of the CMIP3 (IPCC AR4) climate models (http://www-pcmdi.llnl.gov) at the end of the 21st century. For this future simulation, we used an anomaly method to project the IPCC model climates in 2100. This involved considering the 15 'best' CMIP3 models selected in Perkins *et al*. (2012) for the 20c3 m simulations (historical period, 1979–1999) and under SRESA2 scenario (future, 2079–2099). This selection was based on each model skill in simulating relevant climatic features, drivers and variables, which govern the interannual and annual western Pacific climate (Perkins *et al*., 2012). For each of these 15 models, a monthly climatology of the difference between SRESA2 and 20c3 m simulations was computed. These climatological anomalies were then averaged for the 15 selected models. The resulting field was therefore representative of the multi-model ensemble mean changes in seasonal cycle between present day and the late 21st century climate. These seasonal anomalies were then added onto the NCEP2 boundary conditions to provide a new set of condition used to force the WRF regional model. The resulting simulation is hereafter referred as 'CC'. This type of anomaly method is commonly used to avoid the major biases found in direct dynamical downscaling approaches when the modelled present-day states are inaccurate. A very similar approach is used in Knutson *et al*. (2008). A consequence is also that interannual variability largely related to El Niño-Southern Oscillation (ENSO) is assumed to be the same as present in future simulations. This is justified by the lack of agreement between models on ENSO occurrences in the future (Collins *et al*., 2010). To match the present-day REF simulations time-scale, the daily

CC outputs were weekly averaged. Since present model computations were limited to 10 years (1990–1999) due to wave data availability, CC outputs were also analysed for a 10-year time frame (2089–2099).

Results

Hierarchical clustering showed that 39 of the 55 (71%) risk weeks appeared within a 149-week cluster, discriminated at 30% of the maximum distance. This cluster included all the risk weeks for the Hikueru 1994, Manihi 1994, Ahe 2012 and Manihiki 2012 events; plus four Takaroa 2000 event weeks, and three Tatakoto 2009 event weeks. More poorly represented are the 1998 events (Takapoto, Manihi), and the Fangatau 2004 event, with one or two risk weeks. We consider hereafter this cluster (Cluster 1) as representative of potentially lethal conditions, even if all risk weeks were not within 5 weeks of an identified mortality event. Indeed, we did not discard the likelihood that 'false negative' (i.e. unreported events) had occurred for these eight atolls.

The statistics of Cluster 1 (n = 149) vs. all other risk weeks pooled together (Cluster 0) are compared in Fig. 1. The Cluster 1 mean values are higher than those of Cluster 0 for temperature (Fig. 1a) and lower for wind stress (Fig. 1b) and swell (Fig. 1c). The decision tree that compared Clusters 0 and 1 showed that wind stress was the first criteria separating the two clusters, followed by SST and then SWH (Fig. 1d). Three successive thresholds were identified (wind stress < 0.06415 N m^{-2}; SST > 27.38 °C; SWH < 1.034), eventually separating Cluster 1 of 132 risk weeks. This cluster included all the 55 risk weeks.

Spatial autocorrelation maps exhibit distinctive patterns for wind stress, SST and SWH. When considering the R = 0.9 threshold (P < 0.01), wind stress is homogeneous over large areas around the focal atolls, reflecting the lack of orographic effects in an oceanic region (not shown). In contrast, R quickly decreases for both SST

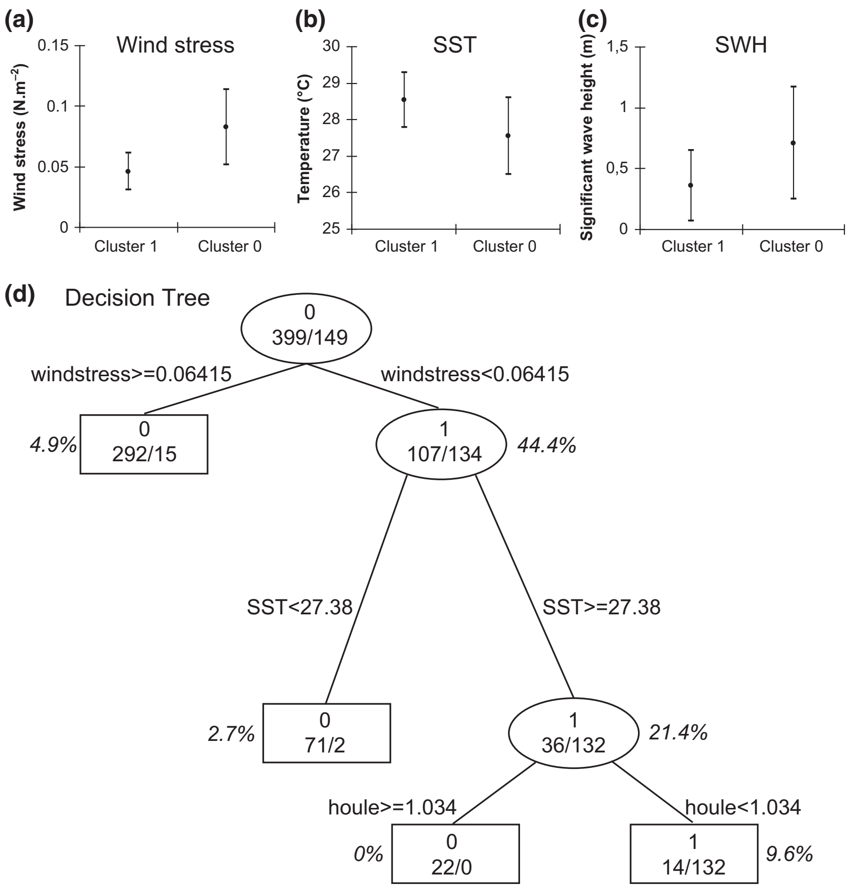

Fig. 1 Mean and standard deviation for (a) wind stress, (b) SST and (c) significant wave height for the Cluster 1 (n = 149, cluster including 71% of the identified weeks before mortality events) and Cluster 0 (n = 399, all other weeks). (d) Decision tree to discriminate the two clusters, using wind stress, SST and significant wave height as variables. The number of samples from Cluster 0 (n = 399) and Cluster 1 (n = 149) at each splitting step is provided, for leafs (square box) or nodes (bubble). Relative error at each node or leaf is provided (in %). The identified thresholds are shown.

and SWH around the focal atoll (Fig. 2). In most instances, $R > 0.9$ is limited to a roughly circular region of less than one-degree radius around the focal atolls, i.e. about 100 km. For $R > 0.95$, only considering extremely similar conditions, the radius is half the size. This suggests that patches of ocean that reach critical SST and SWH values have a limited extent (Fig. 2).

The observed co-occurrence frequencies of the thresholds identified using the decision tree is displayed in Fig. 3 over the 1993–2012 period. The Polynesian region is characterized by a large meridional gradient and a circular gradient around the north Tuamotu Archipelago region. Simultaneous occurrences of all thresholds range from ~10% below the south border of the Tuamotu to ~45% north of that border. This region is indeed sheltered by the large atolls to the south that block the southern swells (Andréfouët *et al.*, 2012; Fig. 4, lower panel). The shape of this high-risk zone is reminiscent of the shape of the warmest temperature tongue that extends climatologically from the western Pacific warm pool to the eastern Pacific in the South Pacific Convergence Zone (SPCZ) region (Cai *et al.*, 2012). However, while the frequency of occurrence of the critical SST threshold alone varies from 40% to 80% in the region (Fig. 4, upper panel), the combination with the wind stress threshold (Fig. 4, middle panel), and then with the significant wave threshold (Fig. 4, lower panel) decreases drastically the overall risk, which becomes patchy at the archipelago scale (Fig. 3).

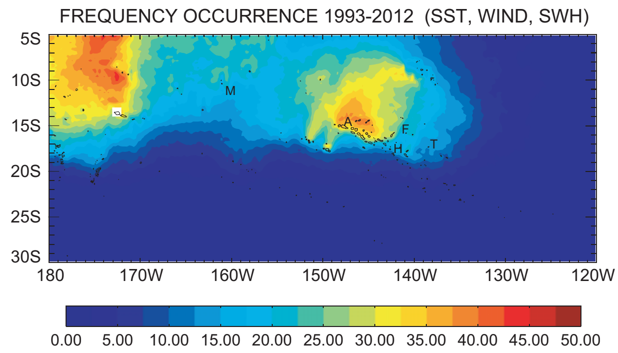

Fig. 3 Observed frequency of co-occurrence of the SST, wind stress and significant wave height thresholds for the 1993–2012 period. M, Manihiki; A, Ahe; F, Fangatau; H, Hikueru; T, Tatakoto.

From the 1993–2012 observations, half of the eight identified atolls (Ahe, Manihi, Takapoto and Takaroa) are within a high frequency zone (>40% of multi-factor occurrences). All others, including the isolated Manihiki in Cook Islands, lie in a moderate frequency area (15–20%). Manihiki lies between the high-risk zone of the Tuamotu, and the very high-risk zone north of Samoa-Fiji, which includes atolls from Tokelau and Kiribati (Phoenix group). However, this later zone does not have hydrodynamically closed atolls, and are thus less vulnerable than Tuamotu atolls.

Agreement between present model and observations over the 6 years of overlapping data (1993–1999) are

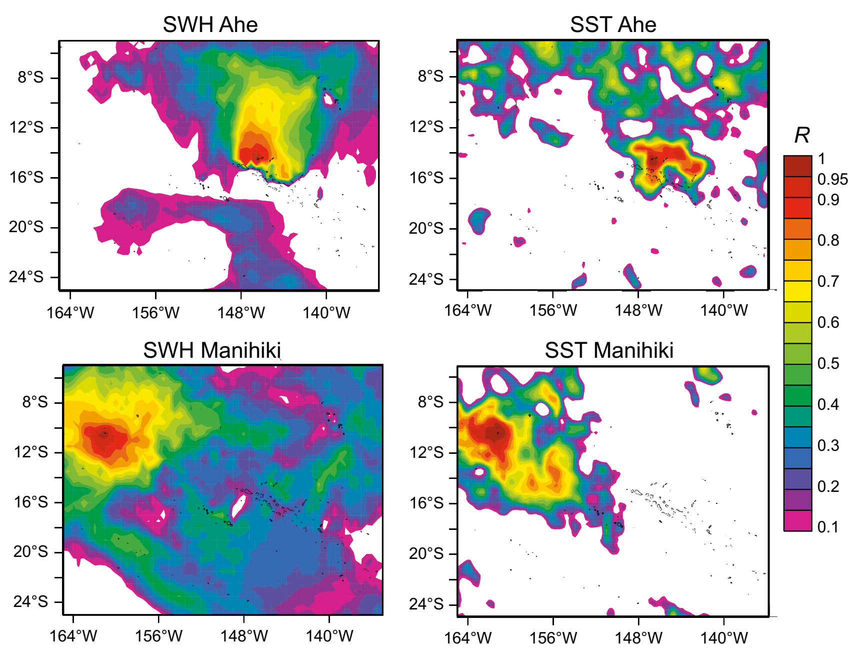

Fig. 2 Autocorrelation maps around Manihiki and Ahe for significant wave height (SWH) and sea surface temperature (SST), both for 5 weeks before the 2012 events.

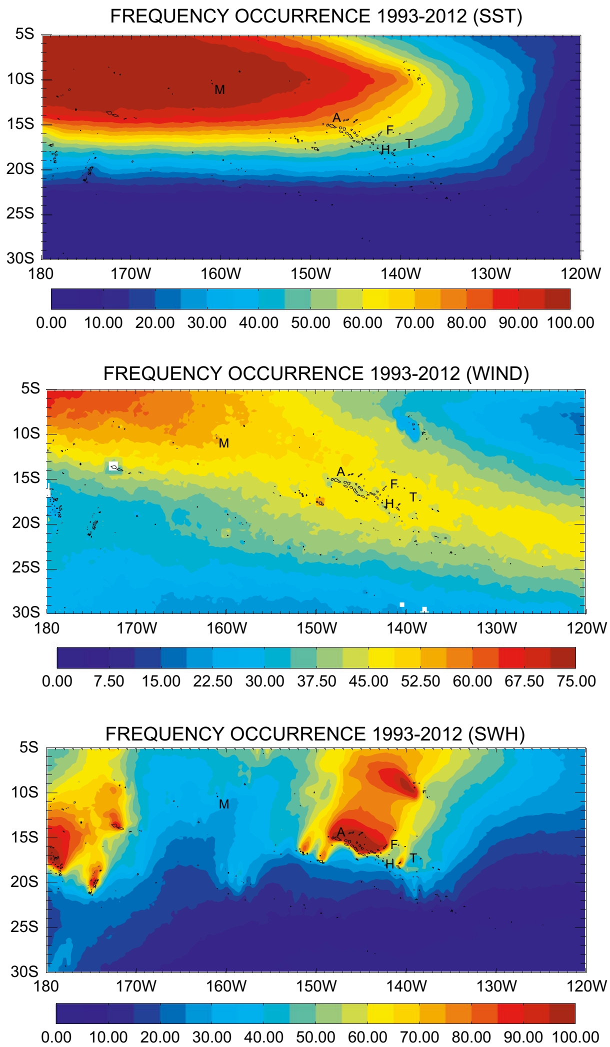

Fig. 4 Observation of the frequency of occurrence of SST (top), wind stress (middle), and SWH (bottom) thresholds for the 1993–2012 period. Compare with Fig. 3 for map of the simultaneous co-occurrence of the three thresholds. M, Manihiki; A, Ahe; F, Fangatau; H, Hikueru; T, Tatakoto.

shown in Fig. 5a, b. When compared to the 1993–2012 period (Fig. 4), the observed risk over the 1993–1999 period is slightly larger (by about 5–10%), but the general patterns remain very similar. The spatial agreement of the model with observations is generally good ($r = 0.97$, $P < 1e{-}10$) including the high frequency of threshold occurrences around Tuamotu. Immediately north of Tuamotu, the model underestimates the risk frequency, while it overestimates the frequencies between the Tuamotu and Marquesas archipelagos. This regional agreement however provides confidence that the modelled outputs are accurate and representative of the present-day conditions.

Finally, Fig. 5c provides the relative change in risk for the model results. The future risk expands meridionally to the south and zonally to the eastern Pacific at the edge of the warmest temperature tongue that extends meridionally from the western Pacific warm pool to French Polynesia. The rate of increased occurrences is thus variable, but currently medium-risk atolls, such as Tatakoto or Hikueru, show a 60–70% increase. This increase in regions that presently exhibit a low to medium risks (<20%) can clearly be attributed to the SST increase in response to global warming rather than to wind changes.

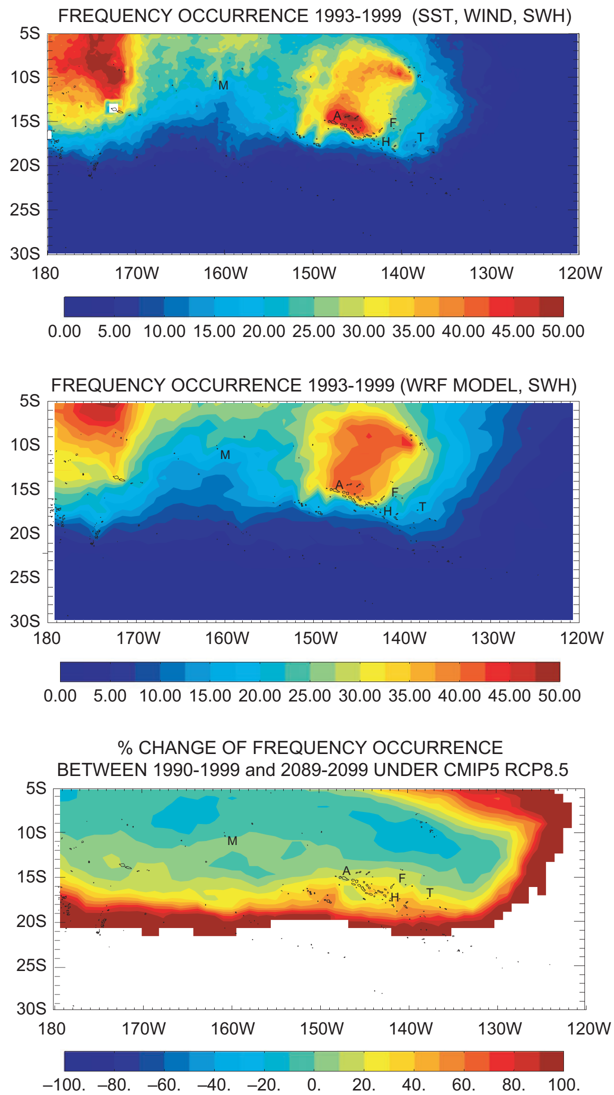

Fig. 5 Comparison between (top) observations and (middle) present-day model results of co-occurrence of the SST, wind stress and significant wave height thresholds over the 1993–1999 period. (Bottom) Relative difference (in percentage) in the co-occurrence of the SST, wind stress and significant wave height thresholds between the model future scenario (SRESA2; 2089–2099) and the model present conditions (1990–1999). M, Manihiki; A, Ahe; F, Fangatau; H, Hikueru; T, Tatakoto.

Discussion

The limited number of events that we could investigate, the likelihood of 'false negative' (unreported events), the uncertainty in the timing of identified events, and the lack of quantification of exact mortality rates, obviously limit the robustness of the conclusions derived from the present analysis. This is in stark contrast with mass coral-bleaching events, for which thousands of local reports were available to infer lethal SST limits (Berkelmans *et al.*, 2004; Baker *et al.*, 2008; Oliver *et al.*, 2009; Hoegh-Guldberg *et al.*, 2011; Lough, 2012). Nevertheless, we were able to narrow the range of environmental drivers that could trigger mass mortality events for semiclosed atolls in the South Pacific. We also show, using spatial auto-correlation that environmental threshold conducive to mass mortality events can occur over small areas, of the order of 100 kms or less. This explains why mortality events are usually restricted to one atoll while others nearby are unaffected. This finding reinforces the hypothesis that exogenous factors reasons (weather), combined with a closed morphology, were the main driver of these events.

The thresholds identified in the present study are observed relatively frequently (Fig. 4; Figure S6), and thus frequent mortalities should occur. In reality, the observed occurrences of mortality are not so frequent. Indeed, for Tatakoto atoll for instance, the climacic giant clam population observed in 2004 (Gilbert *et al.*, 2006) suggests that no mass mortalities had occurred in at least the previous 10-year period. If one event represents 5 weeks of time, this represents a 0.5% frequency of mortality, or, in other words, a 0.5% frequency of simultaneous occurrences of all thresholds. This is two orders of magnitude lower than what observations and model suggest based on actual threshold occurrences and definitions (Figs. 4; Figure S6). This discrepancy can be explained by the heterogeneity of Cluster 1, which included 2/3 of nonrisk weeks. The inferred thresholds are very conservative in this regard. While we conclude that absolute values of frequencies are misleading in terms of actual mortality risk, the relative differences from one area to another are consistent with reports and likely reflect a real hierarchy of risks between different areas. Both observed and modelled present-day spatial patterns are consistent with mortality reports, in particular with the location of Ahe, Manihi, Takaroa and Takapoto in the highest frequency zone. To summarize, a closed atoll geomorphology and the occurrence of the statistically identified thresholds are necessary conditions to build a risk situation, but they are not sufficient.

Based on our analysis, open atolls, flushed by tides or largely open to swells from all directions, are not subjected to mass mortalities. Only small to medium-sized (<200 km^2), asymmetrical, atolls that have their wave-driven aperture in the southern part of the rim seem to be vulnerable. All other atolls are flushed and mixed enough all year which prevents water stratification. If the water is mixed, no anoxic layer can develop. The fact that wind stress is the first factor identified by the decision tree is consistent with this process. Semiclosed atolls become stratified only under calm situations. Otherwise, even weak winds can maintain a low velocity circular current, with surface downwind current and deep currents returning in the upwind direction, sufficient to prevent stratification (Dumas *et al.*, 2012).

The second factor favouring these events is unusually warm ocean temperature. High SST is required to trigger mortalities. High SST in the summer warm season is itself partly the consequence of low wind speeds, with reduced mixing of surface with deeper water, and less atmospheric exchange. Only the May 2012 event in Ahe did not take place during, or at the end, of the warm season. The identified threshold does not seem very high (27.38 °C) since existing measurements in Ahe atoll in 2008 are within this range, even if no mortality occurred (Charpy *et al.*, 2012). However, the Cluster 1 included many nonrisk weeks and more importantly the SST threshold values reflect the cooler oceanic conditions, not the warmer lagoon conditions.

Finally, low swell is the third factor that can be related to mortality occurrences. Lack of swell, especially from the south for asymmetrical atolls, prevents flushing and mixing. For the study area, periods of extremely low SWH occur during austral summer, as well as period of moderate SWH (<1.5 m) coming from both the north and south. In this case, northern swells will not flush asymmetrical semiclosed atolls that are dependent on southern swells for renewal. April generally marks the return of large southern swells and the end of the risk period. However, these high swells may not reach some of the atolls such as Ahe or Takaroa, which are 'down-swell' from other atolls (Andréfouët *et al.*, 2012) and thus remain poorly flushed. This could explain a late event in Ahe in May 2012. Swell can be extremely patchy in the study region, as shown by SWH spatial autocorrelation and risk maps. Low spatial autocorrelation around the atolls was expected for SWH due to the swell shadowing effects in archipelagos, but not for SST, at least to the extent we found here.

Decision tree and autocorrelation maps taken together suggest that a risk situation is due to (i) a regional decrease in trade wind strength, coupled with (ii) local SST rise and (iii) local SWH decrease, all observed during several weeks. This combination of factors explains the singularity of mortality events and their timing. Simultaneous occurrences of adequate thresholds are actually rare and do not occur over large oceanic areas. They also have to occur around atolls which geomorphology makes them vulnerable to mortality events. All these facts quantitatively explain the relative scarcity of these events. In contrast, mass coral bleaching, which is the most studied weather-driven source of coral mortality, is a different process. Although ultimately related to the degree of water mixing, coral bleaching occurs both at a much patchier scale locally and at a large spatial scale regionally. Indeed, it is not necessary to have a stratified lagoon to trigger bleaching (Baker *et al*., 2008). Only locally suitable conditions, typically with both high SST and vulnerable coral communities, are required and bleaching thus varies significantly in space and with depth at local scales. Local patterns can also be related to large-scale environmental factors such as high SST, and bleaching has been related to a number of regional SST-derived, time-integrated, thresholds. However, the accuracy of the SST-derived models is far from perfect when examining local scale data, and poor results have also been reported (Berkelmans *et al*., 2004; McClanahan *et al*., 2007; Weeks *et al*., 2008; van Hooidonk & Huber, 2009; Teneva *et al*., 2012). Thus, even with larger data sets, there is still a large uncertainty when trying to relate mortality events with environmental conditions, and our study necessarily suffers from the same limitations.

We did not try to estimate risks calculated directly from IPCC climate models given the poor performances of several of these models in the tropical Pacific region (Brown *et al*., 2013) and the precision required in model data to reach the identified thresholds. Rather, we believe that our methodology, based on multi-model anomaly downscaling using a state-of-the-art regional model closely related to observations, allows us to bypass the poor performances of the IPCC climate models in the South Pacific. It is worth noting, however, that these models show relatively good agreement on projected SST patterns for 2100 under the SRESA2 (CMIP3) or RCP8.5 (CMIP5) scenarios (e.g. Power *et al*., 2013). To check the robustness of our results using CMIP3 models with CMIP5 models, we recalculated the risk maps with the same thresholds as stated earlier but replacing in the modelled risk calculation the CMIP3 (SRESA2-20c3 m) 15-model ensemble SST anomalies by SST anomalies from a 9-model CMIP5 ensemble (RCP8.5-historical, from bcc-csm1-1, CanE SM2, CNRM-CM5, inmcm4, IPSL-CM5A-MR, IPSL-CM5B-LR, MPI-ESM-LR, MRI-CGCM3 and NorESM1-M.). Using this different suite of models, the relative evolution of risk between present and future was very similar to the one found with CMIP3 models (see Fig. 5c). The largest risk increase is similarly located at the margin of the warm water tongue that extends from the equatorial western Pacific to French Polynesia. This is largely driven by the SST increase in these regions.

Despite their low statistical robustness due to limited documented case studies, the results presented here elucidate a number of mechanisms and minimum conditions that can trigger mass mortalities in poorly flushed lagoons. Both in French Polynesia and Cook Islands, managers take these events seriously, because they have recently impacted local black pearl farmers, who provide a significant fraction of these countries' income (Andréfouët *et al*., 2013). Hoping to solve the issue, inhabitants are eager to dig channels between the lagoon and the ocean to enhance water renewals in calm periods. Authorities may authorize this, but the ecological and hydrodynamic consequences of such modifications are unknown. They could be counterproductive for the lagoonal ecosystems in the long term, if the water residence time is modified. We believe additional knowledge is necessary. Capturing the dynamics of mortality events should be a priority. Indeed, the main gap we identified is the lack of *in situ* biological and physical data in the critical summer period, before the event has reached its climax of mass mortalities. Without these data, mechanisms and precise thresholds cannot be identified, and remediation, if any, cannot be suggested.

Since 2012, three atolls identified here (Tatakoto, Takaroa and Manihiki) have been equipped with pressure and temperature sensors that are locally managed. This is a beginning, but still a modest effort. Other *in situ* data are critical, including at least, but not limited to, chlorophyll and oxygen at various locations and depth. Furthermore, other satellite and model data not considered in the present study may potentially be useful to better characterize and discriminate the events. These data include satellite chlorophyll, rainfall, cloud cover and surface current (Maina *et al*., 2008). Some may covary with SST, SWH and wind stress (Lo-Yat *et al*., 2011) but can he helpful to characterize how a specific event unfolds. Here, considering the limited temporal coverage of satellite Chl-a data (starting end of 1997 for SeaWiFS and in 1999 for Modis) and high-resolution rainfall data (starting in 1998 from the TRMM mission), we did not re-analyse the eight 1998–2012 events using five parameters (SST, SWH, Wind, Chl-a and rain). The large number of entry parameters combined with a low number of mortality events over the period when all datasets were available would likely lead to an overdetermined mathematical problem. It will be obviously a serious commitment for Pacific Ocean countries and for scientists to run an observatory for remote lagoons at risk. While countries have developed networks of observations (French

Polynesia) and automated sensors (in Manihiki, Cook Island), these initiatives were not maintained long enough to provide the cues needed today to fully characterize the risks and help sustain unique local livelihoods.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location map of Pacific Ocean atolls named in the text.
Figure S2. Example of mass giant clam mortality in Tatakoto atoll.
Figure S3. Semiclosed atolls and their geomorphology viewed using satellite images.
Figure S4. Diagram showing the time period covered by observational and model data sets.