Coral bleaching at Low Isles during the 1928-9 Great Barrier Reef Expedition

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Abstract

The Great Barrier Reef Expedition (1928-29) observed two of the earliest known examples of coral bleaching during a 13-month stay on Low Isles, northern Great Barrier Reef, Australia. The first was during austral summer in February 1929 in a shallow moat and the second during austral winter in June 1929 on a deeper seaward slope. Using Expedition records and modern analytical techniques, we geolocated previously undocumented photographs of bleaching and built a detailed picture of environmental conditions which show that the two episodes were driven by different proximate causes. The February bleaching coincided with highest annual seawater temperatures and Degree Heating Weeks, coupled with early afternoon aerial exposure leading to intense heating in tide pools and corals subjected to high solar insolation. Zooxanthellae densities would also have been at a seasonal low and the corals particularly susceptible to bleaching stress. In contrast in June, the seaward slope, normally submerged during the daytime, was aerially exposed to the afternoon sun and although seawater temperatures were 5°C cooler than in the summer and despite relatively low sun altitudes and insolation in the winter, bleaching and mortality due to solar radiation was clearly visible on faces of exposed corals oriented towards the sun. Whilst reports of widespread temperature driven coral bleaching are commonplace today in an era of global

warming, this paper demonstrates how similar environmental cues were involved a century ago and highlights the additional complexity of coral survival in the intertidal zone.

Keywords: Great Barrier Reef Expedition, Low Isles, temperature bleaching, degree heating weeks, solar bleaching, low-tide exposure, intertidal

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All authors contributed to the study conception, general material preparation, and data collection. PLW obtained and carried out the initial analysis of the tidal record. Data analysis was conducted by RPD. The first draft of the manuscript was written by RPD and BEB and all authors read and contributed to the final manuscript. Supplementary information was provided by TS, RPD and PLW.

Data Availability: All data used in this study are publicly available from the sources cited. Datasets generated during and/or analysed during the current study together with R code are available from the corresponding author on reasonable request.

Introduction

The 1928-9 Anglo-Australian Expedition to Low Isles on the Great Barrier Reef (GBR) was a major advance in the study of coral reefs (Spencer et al. 2021) such that '*the work of the …Expedition ... emphasized for the first time the relationships between reef growth and environment and the critical importance for their study in the field*' (p 434-5) (Stoddart 1969). The many achievements included studies of the role of zooxanthellae in coral nutrition (Yonge and Nicholls 1931a,b), of adult and juvenile coral growth (Stephenson 1931; Stephenson and Stephenson 1933), coral reproductive biology (Marshall and Stephenson 1933), the effects of sedimentation on corals (Marshall and Orr 1931), and quantitative ecological surveys (Manton and Stephenson 1935).

Largely hidden in the abundant datasets were observations of coral bleaching in February 1929 described by Yonge and Nicholls (1931b): '*very many corals exposed to the air and in some cases in the shallow pools were killed* ..' (p 154) and Yonge (1930): '*in February the reef flat on Low Isles was covered with the whitened skeletons of dead corals*' (p 78). The bleaching and mortality occurred in corals in the pools and nearby on areas aerially exposed on low spring tides. Yonge and Nicholls (1931b) attributed the bleaching to elevated sea water temperatures during exceptionally calm austral summer weather. While many corals died, survivors were examined histologically throughout a 14-week recovery period (Yonge and Nicholls 1931b) and temperature experiments performed to examine the mechanisms of zooxanthellae loss. Although not documented in the scientific reports, Yonge (1930) also noted further coral mortality during the 1929 austral winter.

No photographic records of either the February bleaching or the June coral mortality appear in the reports. However recent archival searches have revealed undocumented photographs of extensive bleaching on the Anchorage reefs (Fig 1) during the Expedition's stay. In addition, the discovery and analysis of a record from the Expedition tide gauge at Low Isles have allowed us to recreate a record of tidal heights. Using the record together with detailed reef mapping and levelling data, and individual Expedition members' diaries we located the position and dates of the photographs. We then compiled a 'snapshot' of the environmental conditions preceding, and during, the two episodes of coral bleaching/mortality using the Expedition's sea-temperature records and meteorological observations, together with our tidal analysis and computed values of solar radiation. Finally, we examined how these various factors contributed to explain the observed bleaching.

We hypothesised that the two incidences of coral mortality were preceded by bleaching caused by the combined effects of elevated seawater temperatures and/or solar radiation (Brown et al. 1994; Fitt et al. 2001; Brown and Dunne 2016) and that the relative contribution of these factors differed between the two events.

Materials and Methods

Site and Reef Setting

Low Isles (16.384ºS, 145.560ºE) on the northern Great Barrier Reef (Fig 1) was the Expedition headquarters and the site of many of the biological studies. While ecological studies largely focussed on three Traverses (MS 1-3, Fig 1), experiments and regular monitoring of corals were generally in shallow reef areas, particularly in the Western Moat and around the Anchorage. Our use of reef zone terminology follows that of Manton and Stephenson (1935).

Use of a Common Datum for Tidal and Reef Heights

In the scientific reports of the Expedition the heights/depths of reef and island features were recorded relative to a datum established in 1905 by HMS Penguin (Spender 1930b,1932; Manton and Stephenson 1935). Since the purpose of our tidal analysis was to compare sea level heights from the tide gauge record with these reef heights, the tide gauge zero (TGZ) datum, which was 35.36 cm lower than the Penguin datum (Spender 1932) was used as the reference level. Surveyed heights were adjusted to this datum and imperial measurements converted to metric units. The Expedition tide gauge record and all times used in this paper are in Australian Eastern Standard time (AEST) (UTC +10 hrs).

Archival Photographs

Searches of the Sir Maurice Yonge archive at the British Museum of Natural History (BMNH) revealed two undocumented photographs depicting extensive bleaching on intertidal reefs during the Expedition's stay (Photographs F10/F11). The archive contains no further information for either photograph, but accounts of the Expedition (Yonge 1931; Clifford and Clifford 2020) together with times of aerial exposure of the reef, enabled us to confidently identify the date/time of these images.

Tide Gauge Data and Analytical Procedures

Details of the tide gauge and its deployment can be found in Spender (1932) (see also Online Resource). A search of datasets at the British Oceanographic Data Centre (BODC) located a manuscript tabulation of hourly tide data corresponding to the original recording trace (4 February-24 July 1929), now lost, together with analysis by the Liverpool Observatory and Tidal Institute. This record has been digitised and lodged with BODC (Accession POL210202). The record was used to identify the positions/dates of photographs showing coral bleaching, and a 1-minute interpolation produced with the TASK toolkit program (Marine Data Products Team 2017) a 1-minute interpolation was used to extract times when reefs in the photographs were aerially exposed.

Because the tide gauge record only spanned part of the 13 months when the Expedition was on Low Isles (July 1928-July 1929), it was not possible to use the observational record to identify periods of reef exposure prior to February 1929. The hourly record was therefore analysed with U-Tide (Codiga 2011) in Matlab© omitting secular trends and using the Foreman (1977) method (Rayleigh criterion=1) resulting in 59 harmonics. The semi-annual sea-level cycle (Ssa) was included, but not the annual (Sa). Seven principal harmonics (M2, S2, K1, N2, O1, P1, K2) computed by Spender (1932) were in close agreement with our results. The harmonics were used to generate predictions for 1928-1929. The Root Mean Square (RMS) error between predicted and observed tide heights was 9.7cm, possibly due in part to low-frequency (seasonal) signals not fully captured by our analysis. Seasonality was examined using a 25-year (1996-2020) tide gauge record for Cairns ~60 km to the south (https://www.data.qld.gov.au/dataset/cairns-tide-gauge-archived-interval-recordings) Sa= 9.28±2.64cm (mean ±SD) and Ssa= 2.64±1.7cm, with peak sea level in March (Online Resource Fig S14). This compares with amplitudes for Sa=8.57cm and Ssa=2.61cm from Tsimplis and Woodworth (1994).

Sea Temperature and Meteorological Records

We used Expedition sea temperature data, 7 August 1928-21 July 1929, (Orr and Moorhouse 1933) recorded daily (09:00 and 17:30) at the surface and 1 metre depth at a buoy in the Anchorage. Water depth was a minimum of 1 fathom (1.83 m) at all tidal states. Measurements were made with a Petersen-Nansen insulating water-bottle (Knudsen 1923) and a standard centigrade thermometer or a Negretti & Zambra surface water thermometer.

A measure of accumulated heat stress, Degree Heating Weeks (DHW), was compiled using the daily 17:30 readings and the Maximum Monthly Mean Sea Surface Temperature

(MMMSST) of 28.88ºC for the 5km grid square centred on 16.375ºS 145.575ºE from the Coral Reef Watch (CRW) satellite coral bleaching stress monitoring products (version 3.1) (Liu et al. 2014). 'Hotspot' values were computed as the amount by which the 17:30 daily surface temperature was above the MMMSST, and DHW obtained using the same methodology as CRW but over time periods of 30 and 7 days. The choice of these time periods was based on earlier findings that bleaching of corals on reef flats exposed to elevated sea surface temperatures can manifest itself within just a few days (Brown et al. 1999).

Seawater temperature in a 30cm deep coral pool in the Western Moat was also recorded hourly over 1-day periods on 2 October and 25-26 November 1928 by Orr (1933) using an insulated water bottle close to the bottom, irrespective of the tidal height. Daily records of rainfall, wind speed and direction, sunshine hours, and air temperature at Low Isles sand cay from 1 August 1928 to 22 July 1929 were obtained from Orr and Moorhouse (1933).

Solar Irradiance/Insolation

Monthly sun altitude and azimuth for a calendar year were computed for Low Isles (16.384ºS, 145.560ºE) using R package 'solaR' (Perpiñán Lamigueiro 2012) and function 'calcsol'. Sun altitude and azimuth data and daylength (sunrise to sunset) were computed using R package 'suncalc' (Thieurmel and Elmarhraoui 2019).

Solar irradiance on a specific day at a particular location on the earth's surface is fairly constant from year to year, varying mainly due to atmospheric conditions, e.g., cloudiness, haze, water vapour, etc. Data from another year can therefore be used to estimate the maximum irradiance and insolation on a particular day during the 1928-9 Expedition. As a proxy for solar irradiance at Low Isles, we used the nearest available data from Cairns Airport (16.87ºS, 145.74ºE), ~60km south of Low Isles (Australian Government Bureau of Meteorology 2021b), comprising mean 1-minute solar irradiance for 1998 measured with a calibrated pyranometer (wavelengths 0.3-3.5µm). The data was validated against satellite computed daily mean solar insolation (2007–2021) for the Low Isles Lighthouse (Australian Government Bureau of Meteorology 2021a) (Online Resource Fig S10).

Maximum irradiance for each spring tide period was obtained from the nearest clear sky day in the Cairns data (Online Resource Figs S2-9), and insolation was integrated over a time period when the reef was subaerially exposed. If the Expedition sun hour record indicated this was a largely cloudless day, this value was assumed to be reasonably accurate. On other days, since it is not known when any periods of cloudiness occurred, this method is unlikely to be accurate, nonetheless, it is possible to obtain some measure of the potentially damaging effects of solar radiation.

Results

Physical Variables

The Tidal Form at Low Isles

Tides at Low Isles (Fig 2a) are mixed, mainly semi-diurnal (two high tides per day with one higher than the other) with a spring tidal range of 168.5 cm and 42.4 cm at neaps. The lowest daytime spring tides occur in austral winter (May, June, July) (Fig 2b) whilst in the summer months of November to February the lowest tides are at night (Fig 2c). Consequently, the reefs are protected from seasonal highs of temperature and solar irradiance in the summer by deeper water during the day. This tidal pattern meant that during the summer months most studies on the exposed reef had to be conducted at night (Spender 1930a; Yonge 1930; Spender 1932).

Sea Temperature at Low Isles Anchorage and Air Temperature

Both sea temperature and maximum air temperatures showed a seasonal pattern with highest temperatures in the austral summer (Fig 3). Air temperature displayed considerable variation from day to day, presumably driven by the large temporal variation in sunshine hours (Fig 6 below).

Degree Heating Weeks

Degree Heating Weeks mainly accumulated between January and March 1929 (Fig 4), peaking on 16 February, and preceded by a steep rise commencing on 9 February using both the 30-day and 7-day metrics. Either side of this period, water temperatures were too low to generate daily ‘hotspots’. The DHW 7-day metric identifies two main peaks, the first on 24 January (1.66ºC weeks) and the second on 16 February (2.77ºC weeks), which are masked in the DHW 30-day record by the longer cumulative period.

Western Moat Coral Pool Temperature Measurements

The water temperature of a coral pool in the Western Moat (Fig 1 for location) was measured hourly between 00:00 and 23:00 on 2 October 1928 (Fig 5a). This area was submerged except for 3 hrs between 02:41 and 05:42 when the pool was isolated from the open sea. The temperature of the coral pool fell during the early hours from 25.20ºC at midnight to 22.50ºC at 06:00, with a noticeable temperature drop whilst the pool was exposed to the night air. At the nearby Anchorage, bulk surface sea water temperature at 17:30 on 1 October was 25.48ºC.

As the early morning tide covered the pool, the temperature rose to 25.35ºC at 09:00, mirroring the temperature in the Anchorage (25.35ºC) (Fig 5a). During the day with the pool submerged the temperature rose steadily to 28.55ºC at 16:00. The Anchorage temperature reached 28.75ºC at 17:30. The pool remained submerged for the rest of the evening.

On 25 November, measurements commenced at 19:07 (Fig 5a) whilst the coral platform was submerged (Fig 5b). The platform emerged at 23:13 and remained above water until 03:54. The pool temperature at 19:07 was 28.30ºC, mirroring the Anchorage temperature of 27.78ºC at 17:30. The temperature then fell overnight, dropping to 25.30ºC towards the end of the period of exposure. As the sea covered the platform, the temperature increased to ~27.50ºC by 09:00 when the Anchorage temperature was 27.54ºC. The platform was then submerged until 13:19 when it was exposed for 102 minutes until 15:00. As the tide fell the pool temperature rose markedly from 29.09ºC at 11:22 to 34.90ºC at 14:32 when it was isolated from the sea. Orr (1933) recorded a maximum of 35ºC before it was submerged by the rising tide. By 17:31 the pool temperature had fallen back to 28.13ºC and the Anchorage temperature was 28.22ºC. Orr (1933) also reported that the maximum temperature recorded in the coral pool was 37.10°C during hot weather near the end of austral summer.

Sunshine Hours and Solar Insolation

In October the sun is in the northern hemisphere relative to the Low Isles latitude (16.384ºS). It then passes overhead in early November and into the southern hemisphere until early February when it once again passes overhead as it moves back towards the Tropic of Cancer (23ºN). The highest possible sun altitudes therefore occur twice yearly at these times (Online Resource Fig S1).

Sun altitude dictates the maximum possible solar irradiance/insolation, subject to actual weather conditions. The latter can be inferred from the Expedition sunshine record (Fig 6). This is not a timed record so it must be assumed that days with low values may have been overcast during the reef exposure period. Conversely days with high values are likely to have experienced clear sky conditions. Day length during the austral summer varies between 12.3

hrs in October, rising to a maximum of 13.1 hrs in December, and shortening again to 12.5 hrs in February. The record demonstrates high variability throughout the year. Although individual days in the austral summer months have the highest sunshine hours, high variability results in lower average values over spans of days compared to spring and winter.

The February 1929 Coral Bleaching

Yonge and Nicholls (1931b) observed that '*During the full moon spring tides in February, 1929, ... the temperature at low tide during the day in the pools on the reef flat .. rose to very high figures, the highest recorded for the year. On February 22nd .... the temperature ... was literally hot to the touch, and a maximum thermometer reading of 35.1°C was obtained. There was good reason for thinking that the temperature two days previously had been still higher, but unfortunately no thermometer readings were taken on that day*' (p 154-155).

Yonge (1930) reported '*whitened skeletons*' (p 78) appearing on the reef in February 1929, with the full extent of the bleaching revealed on the next low spring tide in March when '*great numbers of whitened skeletons killed by the great heat a month previously were seen. In addition there were a number of other corals, prinicipally species of Favia and Goniastrea which were equally white but which on closer examination were found to be alive and apparently perfectly healthy but with colourless transparent tissues. They resembled in every way corals ... whose tissues ... were almost or entirely without zooxanthellae*' (p 155) (Yonge and Nicholls 1931b). Many of these however recovered their zooxanthellae over the following 14 weeks. Stephenson and Stephenson (1933) also noted mortality of corals in their coral growth '*pens*' (Fig 7) in the Western Moat on 28 February 1929 which they attributed to the period of '*unusually hot weather coinciding with spring tides*' (p 173). The report of this bleaching in February 1929 does not mention the location where it occurred other than referring to '*very many corals exposed to the air and in some cases in the shallow pools were killed at this period*' (p 154) (Yonge and Nicholls 1931b) and to the '*reef flat*' (p 106) (Yonge 1930).

The location may however be deduced to be in the Western Moat. Orr had conducted his physical measurements in a shallow coral pool there in October and November 1928 (Orr 1933) adjacent to traverse MS1 (Manton and Stephenson 1935), to which Yonge and Nicholls specifically referred in their report of the bleaching. The area is characterised by coral platforms and pools in '*a continuous pool .... lying just inside the western part of the rampart* *and boulder tract; … a foot deep* [30 cm] *or rather more in its deeper parts*' (p 46) with a '*very considerable number of coral species*' (p 49) (Fig 7) (Stephenson et al. 1931).

The pools where the bleaching occurred lie in the deeper part of the Moat between 157-195 m along the traverse MS1. In this region Manton and Stephenson (1935) described water moated for up to 5.5 hrs during low tides. The pool bottoms lie at a mean height of 94.5 cm above TGZ with the tops at 122.8 cm as deduced from Spender's detailed survey in Manton and Stephenson (1935). The mean pool depth of 28.3 cm accords with the depth of 1 foot reported by Stephenson et al. (1931) and the minimum water depth of 28.5 cm recorded by Orr (1933).

Tidal levels fell below the height of the coral platform in the Western Moat on two spring tidal cycles in February 1929. At this time of the year (austral summer) the largest spring tides occur during the night so that only during the second cycle was the platform exposed during daytime (20^{th}-25^{th}) (Fig 8). This accords with Yonge and Nicholls (1931b) whose observations of daytime temperatures in the coral pools coincided with the '*full moon spring tides*' (p 375), the timing of the full moon being on 23 February.

We can therefore be certain that the February 1929 bleaching occurred during the daytime low tide exposure between 20-25 February.

The June 1929 Coral Bleaching

An archival photograph ('MY') shows a female expedition member, believed to be Mattie Yonge, on the reef at low tide (Fig 9). On the edge of Low Isles sand cay is a tripod structure which is the tide gauge platform that was erected by 4 February 1929. The photograph is clearly taken from the reef bordering the eastern side of the Anchorage at the approximate position shown in Fig 1 (see also Online Resource Figs S20 & S21).

A second photograph ('LM') (Fig 10) is of exposed reef looking towards the 'Lonely Mangrove' in the background, the position of which is documented on the Key Chart of Stephenson et al. (1931) (Fig 1 for location). Since the foreground or mid-distance does not include open water it can be deduced that this photograph was also taken from a location on the reef bordering the eastern side of the Anchorage, probably not far from the MY photograph. The two photographs also appear in sequence in the BMNH archive, suggesting that they may have been taken on the same date. In both there is evidence of coral bleaching, particularly in the apical parts of the highest branching *Acropora* and also on the marginal edges of north facing massive corals (Fig 10).

In the background of the MY photograph the reef next to Low Isles sand cay is also exposed. This is close to the position of Traverse MS2 (Manton and Stephenson 1935) (Fig 1). The distribution of coral species across Traverse MS2 (Plate VII of Manton and Stephenson (1935)) contains a zone where *Acropora spp.* is abundant between 91 and 146m along the traverse. The MY photograph and foreground of the LM photograph also appear to be in a zone rich in *Acropora spp.* and it is likely therefore that they lie at a similar tidal height. The exact position North-South along the reef edge is not important since this zone lies at a consistent depth.

On traverse MS2 (Manton and Stephenson 1935) the *Acropora spp.* zone is at a mean height of approximately 44cm above TGZ. Manton recorded this as the "*top of rocks and coral*". Stephenson also documents that '*The landward region uncovers at any tide which falls to a level 0.8ft above datum* [60cm TGZ]. *The seaward part is submerged at such a tide, but at the lowest springs (the extreme record being 0.4ft below datum* [23cm TGZ]*) its highest parts are exposed; its deeper regions are therefore always submerged'* (p 62) (Stephenson et al. 1931).

It is evident therefore from these accounts and the heights on traverse MS2 that the *Acropora spp.* zone was only uncovered on the lowest spring low tides. These tides only occurred in daytime in June and July 1929 (Online Resource Fig S15b).

Examining the tidal plots for June and July 1929 in more detail, the days when aerial exposure of the reef occurred were limited to 6 and 7 June, and 6 and 7 July (Online Resource Fig S16). The minimum tidal levels were recorded as 33cm on 6 June, 30cm on 7 June and 41cm on both 6 and 7 July.

The exact dates of the photography can also be narrowed down from accounts of the Expedition work (Yonge 1931; Clifford and Clifford 2020). Between 5-8 July 1929, many of the Expedition members were absent from Low Isles. Over this period, Mattie Yonge was hospitalised on the mainland between 2-9 July and did not return until 16 July. In addition, meteorological data from the island indicates that the weather was windy at the time which does not correlate with the calm conditions in the MY photograph. The photograph is highly unlikely, therefore, to be from 6 or 7 July 1929.

The date of 6 June 1929 is also ruled out since between 5-6 June, Maurice and Mattie Yonge and other Expedition members were visiting Michaelmas Cay and Pixie Reef (Yonge 1931) and did not return to Low Isles until 17:30 on that day, by which time the low tide (33cm at 14:00) had passed and water depths at Low Isles were already between 152 and 210cm.

On 7 June 1929 the meteorological record (Orr and Moorhouse 1933) shows that there were 10 sunshine hours and a SE wind at 8.31 mph (Online Resource Table S2). By the 8 June the wind was freshening (12.39 mph) and sunshine hours declining (6:45) and the following day the wind was even stronger (15.34 mph) with less sunshine hours (1:15). Both photographs show that the sea was calm (mirror-like in the MY photograph) which would be most consistent with 7 June.

The most likely date for the MY photograph is therefore 7 June which coincides with the lowest daytime spring tide of 1929 during the expedition. The low tide was 30.48cm at both 14:00 and 15:00 (and would have been even lower at ~14:30). This photograph had previously been incorrectly attributed to the February bleaching in Spencer et al. (2021) before the tide gauge record became available.

On 7 June the sun rose at 06:50 and set at 17:40. Maximum altitude was 50.9º at 12:10 with the sun azimuth 2.3º (nearly due North on its track from East to West). In the LM photograph a shadow is cast by the coral in the foreground (the photograph is looking in an easterly direction) and solar lesions can be seen on the north face of the coral colony (Fig 10). At the time of the low tide exposure on 7 June (13:27-15:24) the sun would have been at between 47.5-30.4º altitude and 337-310º azimuth so the position of the shadow is quite plausible for a photograph taken at that time on that day, and the orientation of the lesions would also be consistent with this interpretation.

Discussion

Coral Bleaching in February 1929

Yonge and Nicholls (1931b) considered the bleaching and subsequent death of corals they observed on 22 February 1929 was '*to be attributed to the exceptionally high temperature. Exposure to the air or to the intense light could not alone account for so much destruction*'. They reasoned firstly that as regards aerial exposure '*during the winter months very little destruction was observed, although the corals were exposed for much longer periods during the day*', and secondly that '*the light was as intense and the period of exposure as great, and* *often greater, during the other spring tides during the summer, but, as these never happened to coincide with such hot, calm weather, the temperature never rose to the same abnormal height*' (p 154).

They also concluded that water temperature was the cause of the bleaching from subsequent experiments where they exposed colonies of *Favia* (now named *Dipsastraea*) to temperatures of 36^{o}C and 40^{o}C for varying time periods, noting that '*Corals are killed if exposed to high temperatures for long periods, but they can survive moderately high temperatures if only exposed to them for short periods. But in this latter case the zooxanthellae may be expelled, in part or entirely*' (p 169) (Yonge and Nicholls 1931b).

To test Yonge and Nicholls' theories, we posed four questions about the low tide exposure in February 1929 compared to other low tide exposures in the summer months: (1) Was the duration of aerial exposure greater?; (2) Was solar radiation greater?; (3) Were there differences in air temperature or bulk seawater temperature?; and (4) Were coral pool temperatures higher?

Duration of Aerial Exposure

In February 1929 the reef was exposed on 6 consecutive days (20-25th) for a combined total of 722 minutes (Online Resource Table S1). A slightly lower cumulative total occurred in January 1929 (680 mins) and a longer period in October 1928 (780 mins). Maximum daily exposure was also higher in October (162 mins) compared to January (148 mins) and February (146 mins). Thus, Yonge and Nicholls (1931b) were correct to note that longer periods of aerial exposure occurred earlier in the summer.

Exposure to "Intense Light"

In February 1929, the low tide exposure period was largely cloudy except for two days (22nd and 23rd) when sunshine hours were 10:30 (hrs:min) and 9:10 respectively (Online Resource Fig S11). As a result, the maximum solar insolation of 36.28 MJoules m^{-2} (Online Resource Table S1) is very unlikely to have accumulated over the period. Nevertheless, on 22nd the insolation was probably close to the daily maximum of 7.73 MJoules m^{-2} and on 23rd the total was probably only just under 6.43 MJoules m^{-2}. Cumulative maximum insolation in November, December and January were all much lower (between 9.21 and 25.12 MJoules m^{-2}). In October 1928 however the figure was higher (44.3 MJoules m^{-2}) than in February 1929 and moreover sunshine hours were consistently high, varying between 10:50 and 9:30

(Online Resource Fig S12). Daily maximum insolation was also higher (up to 9.62 MJoules m^{-2}).

Unlike these differences in insolation there would have been little difference in maximum solar irradiance between February 1929 and October 1928 as inferred from the highest sun altitudes at the beginning of reef exposure, 79.4º in October and 74º in February both on clear sky days. The assertion by Yonge and Nicholls (1931b) that '*the light was as intense … during the other spring tides during the summer'*, would thus appear to be correct, certainly as far as October 1928 was concerned when there was no recorded bleaching.

Air and Seawater Temperature Differences and Degree Heating Weeks

In February 1929 bulk seawater temperatures at the surface at 17:30 averaged 29.64°C during the exposure period (19-26th) (Online Resource Table S1). In December 1928 and January 1929 the mean seawater temperature was slightly higher (29.72 and 30.29ºC respectively). During these months seawater temperatures are at their seasonal maximum (Fig 3). Comparatively, in October the mean seawater temperature was markedly lower at 26.42ºC.

The temperature stress metric of Degree Heating Weeks shows that immediately preceding the February 1929 exposure, DHW reached its highest annual value (2.77ºC weeks DHW-7) (Fig 4) before declining sharply thereafter. Prior to this, the highest value was on 24 January (1.66ºC weeks DHW-7) also during a period of low tide exposure but at a time when no coral bleaching was reported.

The differences in mean maximum daily air temperature during exposure periods was less marked. In February 1929 the temperature was lowest at 31.59ºC even though this is a month when seasonal temperature is at its highest (Fig 3). In the other months it varied between 33.84ºC in December and 32.66ºC in November. However, when the temperature record for February 1929 is examined in detail it is evident that air temperatures were building through the month until a fall on 20th which coincided with low sunshine hours that day (2:20) and the following day (21st, 5:00) (Online Resource Fig S13). Air temperatures rose again to 33.9ºC on the 22nd, the day that Yonge and Nicholls (1931b) first reported bleaching, when sunshine hours were high (10:30), and the following day (23rd, 34.9ºC and sunshine hours 9:10) before plummeting on 24th and 25th when sunshine hours fell to 0:00 and 0:20 respectively as the weather became unsettled with average daily windspeeds increasing to 11.72 mph on 25th and 22.03 mph on 26th February (Online Resource Table S1). February 1929 does not stand out as exceptional in terms of maximum air temperature on any single day during low tide exposure, with the highest temperature of 34.9ºC on 23 February, also recorded on 24 January and 25 November, and 34.7ºC on 9 October 1928.

Thus, although bulk seawater temperature and air temperature were not abnormally high during aerial exposure of the reef in February 1929 compared to earlier months in the austral summer, nonetheless the cumulative heat stress index of DHW shows that bulk sea temperature is likely to have been a contributing factor in the coral bleaching, certainly as far as the corals growing on the shallow Western Moat coral platform were concerned.

Western Moat Pool Water Temperatures

Also important for bleaching of corals submerged in tidal pools in the Western Moat is the potential for heating of trapped seawater during periods of exposure. Temperatures in the pools were not however monitored on a regular basis during the Expedition and detailed records only exist from the measurements taken by Orr (1933) on 2 October and 25-26 November 1928. Nevertheless, what is evident from Orr's records is that the pool temperatures mirrored the surface water sea temperature at the Anchorage when the coral platform was submerged but during daylight exposure periods, such as on 26 November 1928 when sunshine hours totalled 7:45, the water temperature in the isolated pools was driven upwards by the sun's heating effect (Fig 5).

Thus, on the day when bleaching was observed on 22 February 1929 sunshine hours were high (10:30) and Yonge and Nicholls (1931b) reported that coral pool temperatures rose to 35.1°C and they had good reason to think that it was higher on the low tide two days earlier. Nonetheless this temperature was comparable to that recorded by Orr on 26 November 1928 (35°C) when no bleaching had been noted. We thus conclude, unlike Yonge and Nicholls (1931a) who considered high water temperatures alone to be the cause of bleaching in February 1929, that several factors in combination were likely to have been responsible for both the bleaching of the corals in the pools and those on the adjacent coral platform.

Firstly, cumulative bulk seawater temperature stress (DHW) peaked in late February 1929, rising to its annual highest value. Secondly, solar radiation undoubtedly played a part, both indirectly in the heating of the coral pools at low tide, but also directly through the known damaging effects of high photosynthetically active radiation on coral photosynthesis (Brown and Dunne 2016; Gómez-Campo et al. 2022). Thus, on 22 February 1929 the coral platform was exposed for longer (146 mins compared to 102 mins) than on 26 November 1928 when similar high temperatures had been recorded in the coral pools. Sun altitudes during aerial exposure were also high (74º), and maximum insolation on 22 February was 7.73 MJoules m^{-2} during very high sunshine hours (10:30). This figure can be compared to 5.57 MJoules m^{-2} in November when true values were also likely to have been lower, due to cloudiness (sunshine hours 7:45). Thirdly it is now well known that zooxanthellae population numbers in corals vary by 15-90% on a natural seasonal cycle (Brown et al. 1999; Fagoonee et al. 1999; Fitt et al. 2000) falling to their lowest at the end of the summer (i.e. dry) season during which the corals are subject to consistently high water temperatures and solar irradiance/insolation. Thus, as the end of the austral summer approached in February 1929 the corals would have been particularly susceptible to further damage and zooxanthellae density reduction.

Coral Bleaching in June1929

Compared to the bleaching reported by Yonge and Nicholls (1931b) in February 1929 on the Western Moat reefs, the sun altitude in June is considerably lower than during the austral summer months (Online Resource Fig S1). Maximum daily insolation during exposure of the *Acropora spp.* reef zone on 7 June of 4.32 MJoules m^{-2} (Online Resource Table S2) was therefore 44% lower compared to that experienced by the Western Moat area when bleaching was observed on 22 February 1929 (7.73 MJoules m^{-2}, Online Resource Table S1). However, the days leading up to 7 June 1929 were also subject to high solar radiation (4 days with 9:45 average daily sunshine hours) whilst corals were in shallow water during the middle of the day, and on 6 June aerial exposure persisted from 12:58 to 14:34, when sun altitude was between 50-40º, and solar insolation 4.02 MJoules m^{-2} (Online Resource Table S2).

Additionally, the deeper Anchorage reefs (78.8cm lower than the Western Moat coral platform) were not subject to the same degree of aerial exposure as those in the Western Moat. For most of the year they are always submerged during daylight hours, and only on the lowest winter spring tides, starting in June, are they aerially exposed during the day. Thus, although solar insolation may not have been as great during times of exposure, corals at the Anchorage are likely to be less well acclimatised and therefore more susceptible to its damaging effect (Brown et al. 2002). Bulk mean seawater temperatures at the Anchorage, which undoubtedly were a principal factor in the Western Moat bleaching in February, were also 5ºC lower in June 1929.

The photographic evidence of the June 1929 bleaching also provides clues as to the most proximate cause. Aside from bleaching in apical tips of *Acropora spp.*, the bleaching on massive corals was on their northern surfaces (Fig 10). These surfaces face towards the sun at this time of the year. Furthermore, the asymmetric growth shape of the corals is similar to that seen at Phuket, Thailand which has been conclusively linked to periodic exposure to damagingly high solar radiation (Brown et al. 1994; Scoffin et al. 1997; Brown and Dunne 2016). It should be noted, however, that the directional flow of sea water during an ebbing tide may also be an influence on coral growth on the Anchorage reefs (Scoffin and Stoddart 1978).

It would thus appear that the coral bleaching in June 1929 was primarily driven by aerial exposure and solar radiation in a similar manner to that observed on intertidal reefs in South-East Asia, rather than high water temperatures which were involved in the February 1929 bleaching in the Western Moat. Indeed Yonge (1930) noted this difference in his description of mortality in the winter months: '*During the wonderful low tides in May, June, July and August, when a great wealth of living coral was exposed, deaths occurred, though apparently not to the same extent as during the summer, owing to the lower temperature. Exposure to the sun and air is the restraining factor …* ' (p 78).

How might these bleaching events nearly 100-years ago be viewed in the light of present-day coral bleaching particularly in the context of global warming?

Firstly, there is no evidence that the two bleaching events in 1929 were on the scale of modern-day widespread sea-temperature bleaching. These were events driven largely by microclimates in the intertidal zone resulting from complex tidal variations, with consequent exposure to the air and intense solar radiation and/or to high temperatures in trapped seawater pools. Compared to the subtidal where bulk seawater temperature is the dominant influence on coral health, the environment in the intertidal is thus characterised by transient, rapid and extreme physical fluctuations. Research into mortality risks to intertidal corals has been a niche area of coral research compared to the focus in recent decades on subtidal reefs. Recent 'emersion mortality risk' studies by Buckee et al. (2022) help to address this shortcoming for Australian coral reefs and suggests that the tidal regime has been a fundamental factor supporting the historical bio-geographical development of the GBR.

Bulk seawater temperature nonetheless influences coral health in the intertidal during periods of immersion and provides the baseline on which the stresses of tidal exposure are superimposed. Thus, although low-tide exposure driven bleaching events such as those reported in this paper will have been a recurring feature over historical time and become imprinted on the physiology of corals that inhabit this zone (Schoepf et al. 2020), a warming ocean will nonetheless exacerbate this effect and depress zooxanthellae numbers and affect coral health.

At the same time anthropogenic rising sea level (von Schuckmann and Le Traon 2022) protects intertidal corals from the physical extremes of low-tide exposures and has been shown to promote coral cover (Brown et al. 2011; Scopelitis et al. 2011; Saunders et al. 2015). Indeed, for the GBR sea-level rise modelling under extreme climatic projections (RCP 8.5) projects that reefs will become submerged at a timescale of 100+ years (Morgan et al. 2020). Superimposed on this are fluctuating decadal/intradecadal climatic process such as the Indian Ocean Dipole and El-Niño Southern Oscillation which depress or elevate sea level (as well as sea temperature) in an apparently stochastic manner at scales of months to years and are an important driver of coral cover on shallow reefs (Dunne et al. 2021).

That these observed instances of coral bleaching have occurred since 1929 and will occur in the future is clear. Whether they will increase in frequency due to rising sea temperature or decrease due to rising sea level still remains unknown.

The fact that we have been able to embark on this post-hoc examination of bleaching is a tribute to the meticulous work of the Expedition, including the surveying of the various reef zones. The point was eloquently stated by the Expedition's surveyor, Michael Spender, who observed in 1931 that '*to my mind the most weighty constituent of our joint work* [the biological and the geographical parties] *was that connected with levels. On the results of this expedition, we are able to state, with a high degree of accuracy, that such a part of the reef or such a zone of corals is found at a level so many feet above or below datum or mean sea-level. The value of the accurate relation, where estimation can be so misleading, of organisms to tide levels is readily appreciated. This quantitative work will only fully assert itself when other work is available…* ' (p 99-100) (Spender 1931). Through the painstaking work and careful observations and measurements by the Expedition in 1928-29 together with the re-discovery of the tide gauge record we have been able to undertake this reconstruction of environmental conditions and to interpret the causes of some of the earliest field bleaching episodes on record. The Expedition's records have similarly enabled others to evaluate long-term ecological changes to the shallow reefs (Fine et al. 2019) and to reef top landforms and habitats (Hamylton et al. 2019) around Low Isles.

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Figures

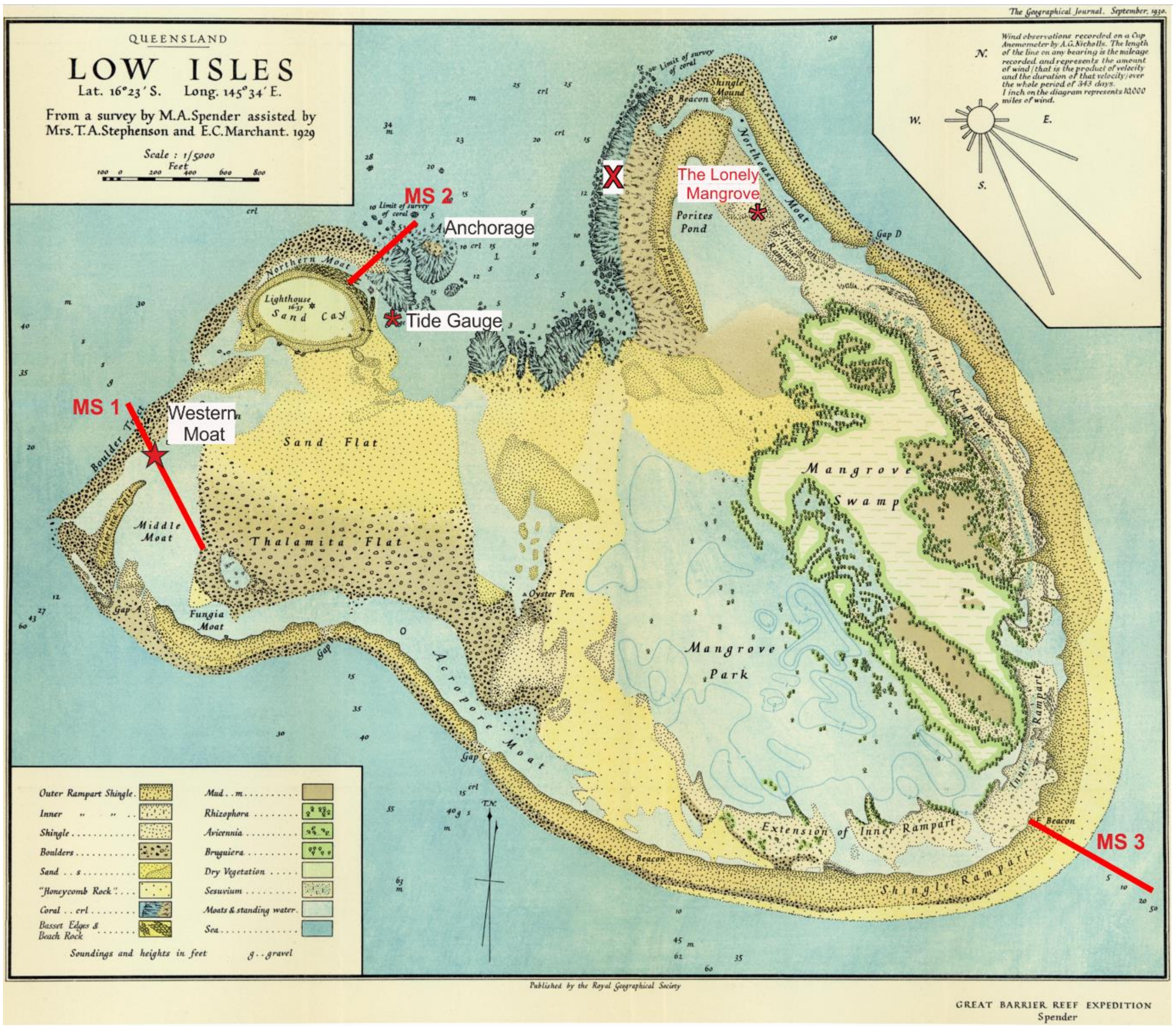

Figure 1. Low Isles from Spender (1930b) showing positions of Traverses (MS 1-3) (Manton and Stephenson 1935), Anchorage, Western Moat coral pool (Orr 1933) (red star), Lonely Mangrove, tide gauge (black star), and estimated position of photographs in Fig 9 & 10 (red cross). Original map by permission of the Royal Geographical Society (with IBG).

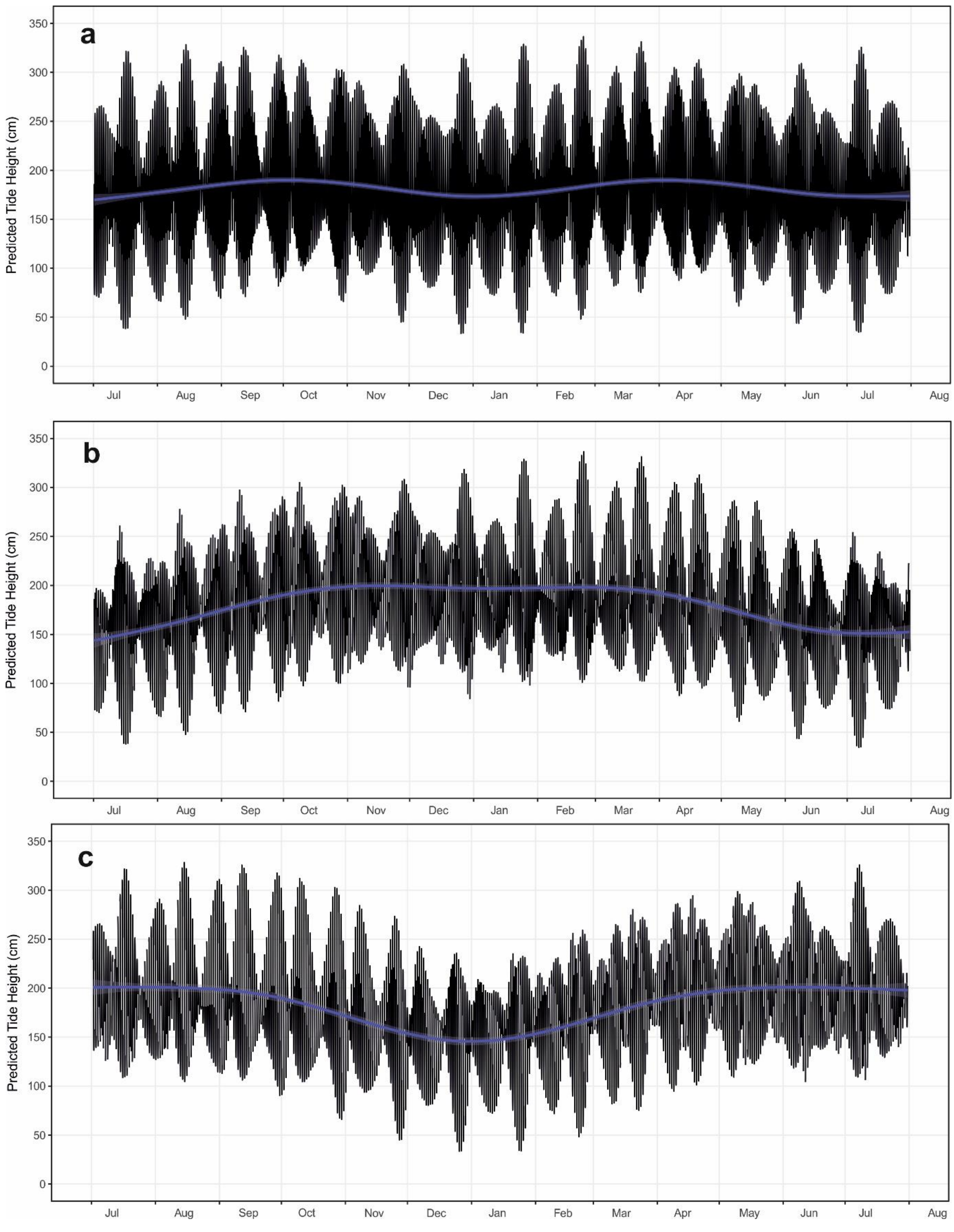

Figure 2. Tidal form at Low Isles (July 1928-July 1929) relative to tide gauge zero. **a.** Full record**. b.** Daytime tidal heights (06:00-18:00). **c.** Night tidal heights. Since the period of tide gauge observations only spanned 4 February–24 July 1929 the one-year record shown uses predicted values from U-Tide. A generalised additive model (Hastie and Tibshirani 1990; Wood 2017) has been fitted (blue line) to illustrate low-frequency trends.

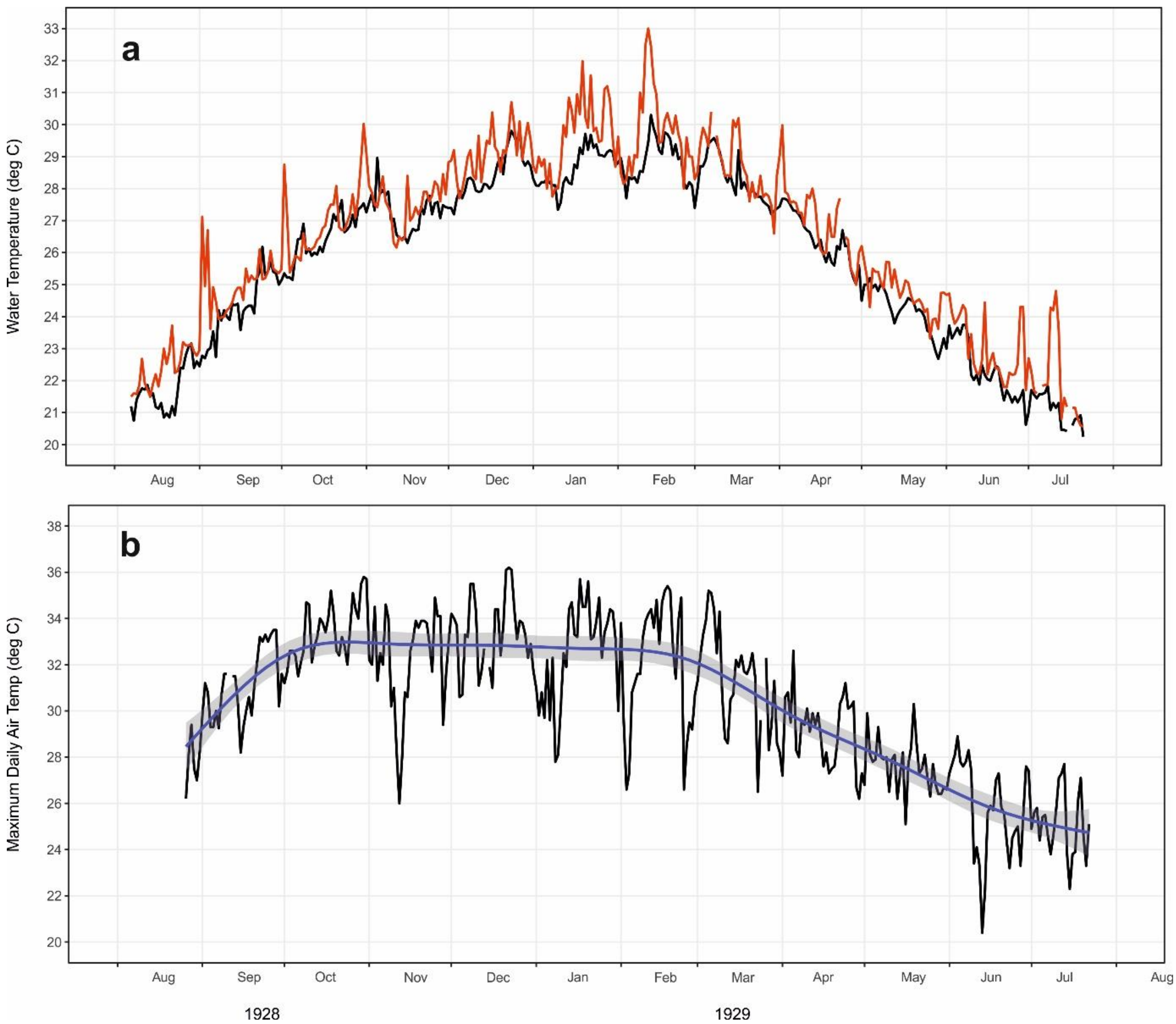

Figure 3. **a.** Anchorage surface sea water temperature (ºC) (7 August 1928-21 July 1929) at 09:00 (black line) and 17:30 (red line). **b.** Air temperature (maximum daily ºC) (7 August 1928-21 July 1929). Line fitted is a Generalised Additive Model (Hastie and Tibshirani 1990; Wood 2017) with 95% confidence interval (grey shading).

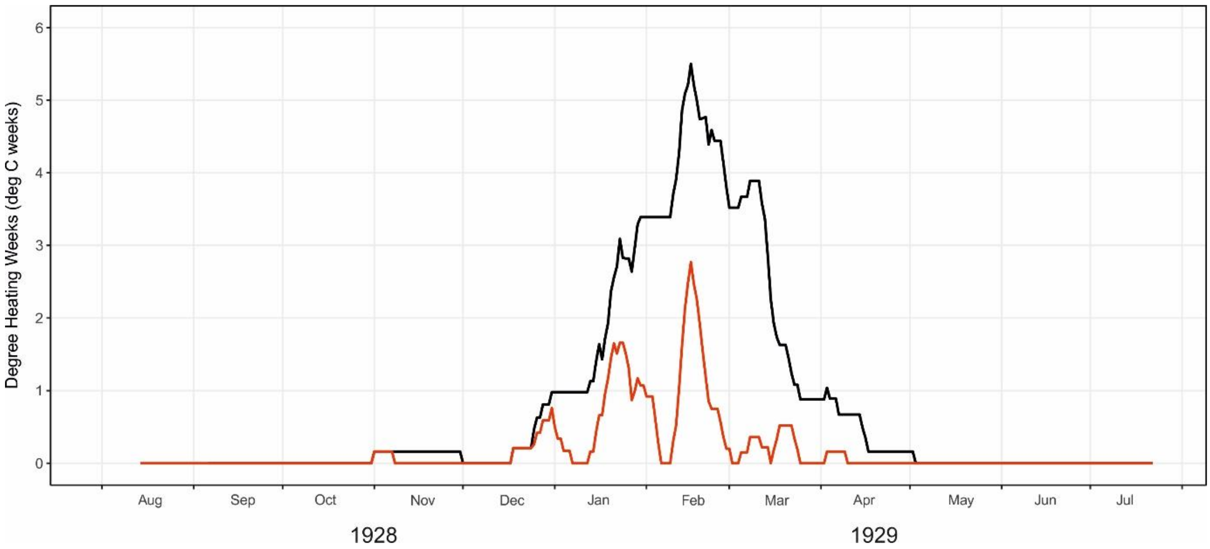

Figure 4. Degree Heating Weeks. Black line 30-day period, red line 7 days. See Materials and Methods for description of methodology.

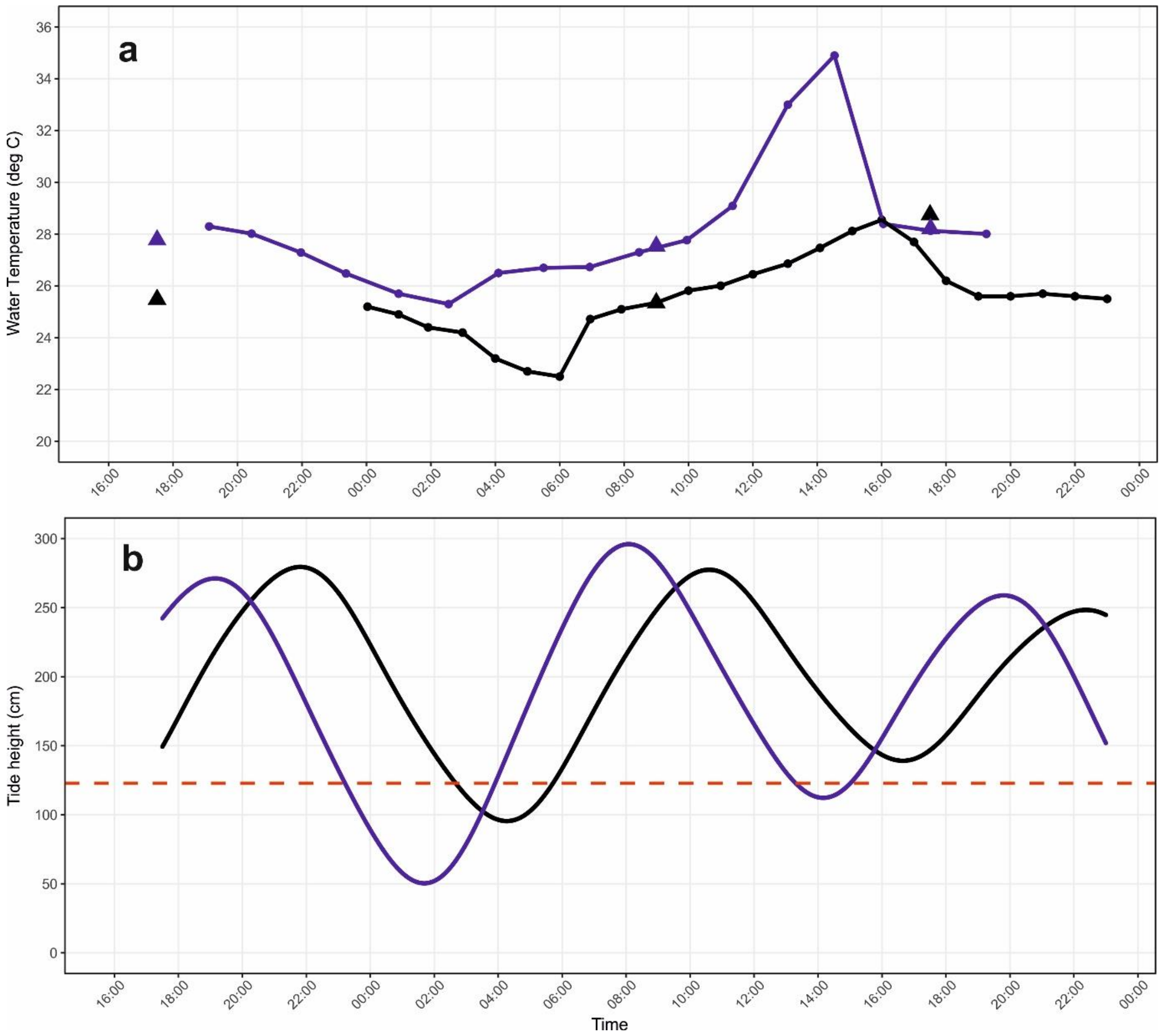

Figure 5. **a.** Water temperature (ºC) in a coral pool in the Western Moat on 2 October 1928 (black line and dots) and 25-26 November 1928 (blue line and dots) (Orr 1933) and temperature at the Anchorage (corresponding diamonds) (Orr and Moorhouse 1933). **b**. Corresponding tidal heights predicted with U-Tide. The red dotted line is the Western Moat coral platform height (122.8cm) (Manton and Stephenson 1935) .

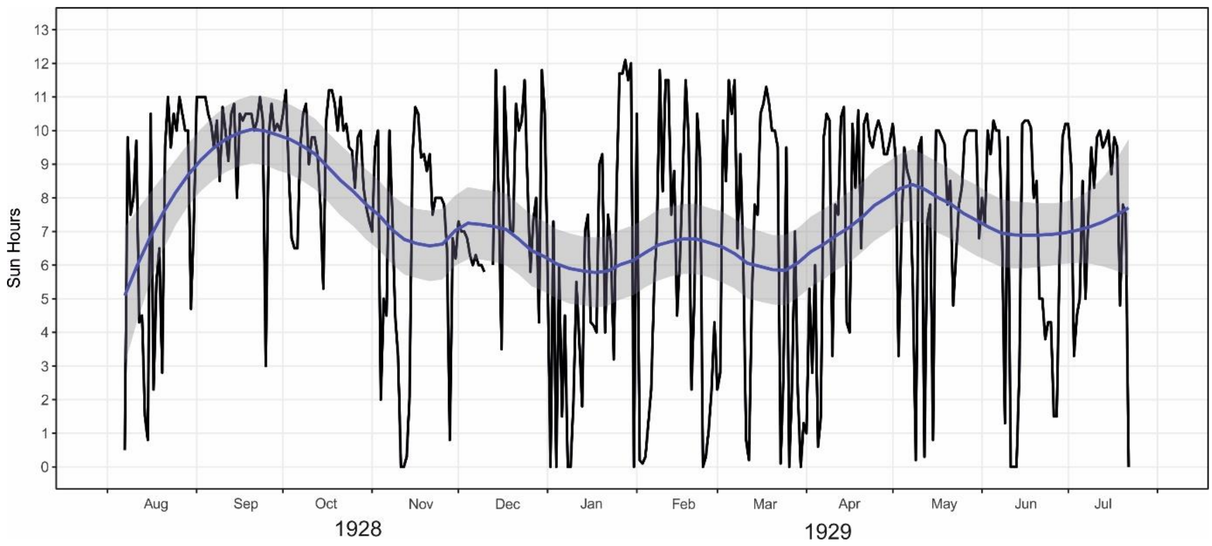

Figure 6. Daily sunshine hours 7 August 1928-22 July 1929 (Orr and Moorhouse 1933). The blue line represents a loess fit using a span of 0.3 with 95% confidence limits (grey shading).

Figure 7. The Western Moat towards Low Isles sand cay at low water. In the Moat are platforms of massive *Porites* with pools between. In the foreground is an enclosure for ecological observations and in the middle distance an enclosed pool where the coral growth experiment of Stephenson and Stephenson (1933) was carried out. Photograph by Sidnie Manton with permission from Mrs J Clifford.

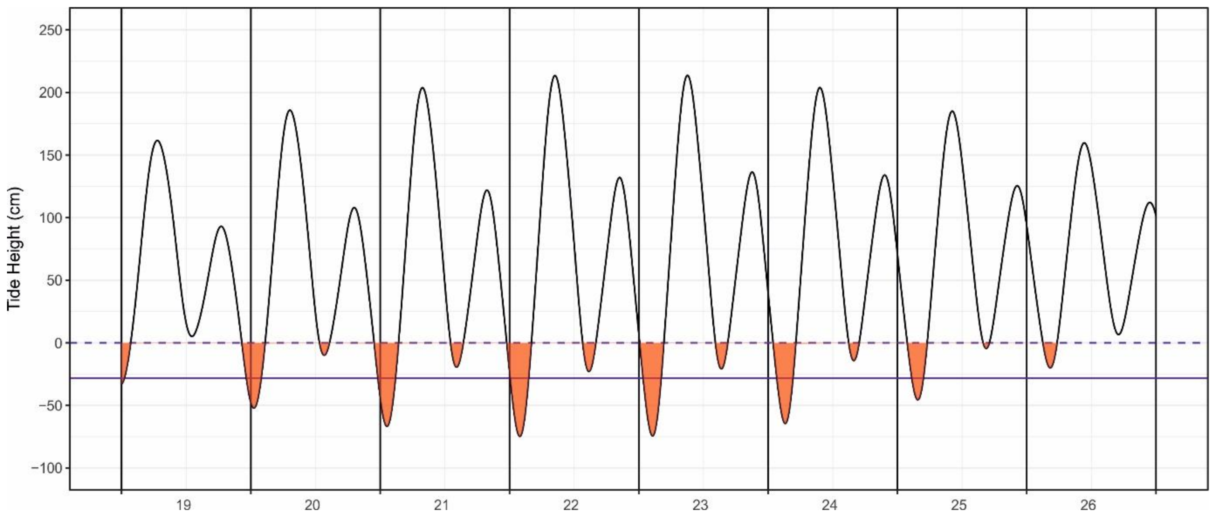

Figure 8. Predicted tidal heights 19–26 February 1929 from harmonic analysis in U-Tide. Levels rebased to the Western Moat coral platform height (122.8 cm, dashed line). The solid line is the bottom of the coral pools (94.5cm). Periods of exposure highlighted in red.

Figure 9. The eastern reef edge of the Anchorage looking WSW towards the Low Isles sand cay. The tide gauge 'tripod' is just visible (arrowed). With permission from Maurice Yonge Collection (BMNH, London).

Figure 10. Exposed coral on the eastern reef edge of the Anchorage looking eastwards towards the ‘Lonely Mangrove’ (black arrow). Bleaching on the north faces of massive coral

indicated by white arrows. The branching coral in the foreground also appears to exhibit some bleaching. The coral in the pool casts a shadow on its southern side (to the right). With permission from Maurice Yonge Collection (BMNH, London).

Coral Reefs

Supplementary Information

Coral bleaching at Low Isles during the 1928-9 Great Barrier Reef Expedition.

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Date	Start time	End time	Minutes exposed	Minimum tide height (cm)	Sun (hrs:mins)	Wind direction & average speed (mph)	Sun at start time		Sun at end time		Max Insolation during low tide period	Air Temperature Max/Min	Anchorage surface water temp (1730)
							Altitude (deg)	Azimuth (deg)	Altitude	Azimuth	MJoules m^{-2}	ºC	ºC
Notes: (1) the red highlighted sun hours are not accurate because the afternoon sun hour data were lost (2) blue text entries are dates on which Orr (1933a) conducted tide pool physical measurements													
October 1928													
2	Not exposed			139.11 at 16:38	11:10	S – 10.22			23.3	272.7		31.7/21.7	28.75
7	10:30	11:29	60	120.54	9:30	W – 3.84	63.5	69.3	75.6	44	3.55	32.1/22	25.85
8	10:40	13:00	141	107.36	10:30	SE – 4.51	66	67	74	307	8.5	32.6/23.5	25.75
9	11:11	13:52	162	99.25	10:50	ESE – 5.56	73	57	63	288	9.62	34.7/23.8	26.6
10	11:48	14:29	162	97.27	9:00	ESE – 6.71	79	28	54	281	9.28	34.6/23	26.1
11	12:31	14:55	145	101.35	9:45	ESE – 9.34	79.4	327	48	277	7.85	32.1/23	26.1
12	13:22	15:11	110	110.62	9:45	E – 14.66	70	293	44.5	275	5.5	32.8/24.1	26.1
13	Not exposed			123.6 at 14:49	9:20	ESE – 15.07			50	277		33.2/23.9	26.18
	Total		**780**						**Cumulative**		**44.3**	**Mean max 32.97**	**Mean 26.42**
November 1928													
5	Not exposed			126.75 at 10:28	5:00	WSW – 6.21			67	92		32.5/26.8	27.42
6	11:03	11:47	45	121.34	4:30	ESE – 4.71	75	92	86	89	2.87	32/24.3	27.9
7	11:40	12:42	63	119.59	10:00	SE – 14.44	84	92	81	268	4.07	34.6/25.1	28.38
8	12:35	13:10	36	121.62	7:30	SE – 9.87	83	265	75	266	2.27	34/25.3	27.6
9	Not exposed			126.61 at 13:30	4:30	SE – 14.02			70	265		30.2/22.8	27.42
	Total		**144**						**Cumulative**		**9.21**	**Mean max 32.66**	**Mean 27.74**
23	Not exposed			123.25 at 11:53	8:00	SW – 4.16			84	140		32.9/24.2	27.9
24	11:51	13:21	91	115.64	8:00	W – 3.52	84	137	72	253	5.79	31.7/24.4	27.6
25	12:27	14:14	108	111.64	8:00	ENE – 3.34	84	223	60	256	6.53	34.9/24.6	27.78
26	13:19	15:00	102	112.26	7:45	ESE – 7	73	251	49	256	5.57	34.1/25.5	28.22
27	14:26	15:37	72	117.75	6:30	E – 4.47	57	256	41	256	3.29	34.1/25.5	28.1
28	Not exposed			127.03 at 15:59	0:45	SE – 9.34			36	255		34.1/25.5	27.6
	Total		**373**						**Cumulative**		**21.18**	**Mean max 33.63**	**Mean 27.87**
December 1928													
23	Not exposed			128.18 at 12:32	10:15	SE – 4.55			82	200		36.1/27.2	29.78
24	12:59	13:54	56	120.03	11:30	WNW – 3.63	79	230	67	248	3.44	34.4/26.7	30.7
25	13:30	15:08	99	113.8	8:30	E – 3.69	72	244	50	253	5.44	33.1/27.3	30
26	14:16	16:08	113	111.11	5:45	W - 4	56	252	37	253	5.22	33.9/26.9	29.04

Date	Start time	End time	Minutes exposed	Minimum tide height (cm)	Sun (hrs:mins)	Wind direction & average speed (mph)	Sun at start time		Sun at end time		Max Insolation during low tide period	Air Temperature Max/Min	Anchorage surface water temp (1730)
							Altitude (deg)	Azimuth (deg)	Altitude	Azimuth	MJoules m^{-2}	°C	°C
27	15:12	17:00	108	112.81	7:20	SW – 4.09	50	253	25	251	3.76	33.8/23.9	30.1
28	16:23	17:37	75	118.42	8:00	SE – 5.03	34	253	17	250	1.67	33.3/24.4	28.9
29	Not exposed			126.04 at 17:58	4:15	SSE – 14.84			12	249		32.3/24.1	29.55
	Total		**451**						**Cumulative**		**19.53**	**Mean max 33.84**	**Mean 29.72**
January 1929													
21	Not exposed			133.22 at 12:49	4:00	ESE – 4.82			85	228		33.1/26.5	29.9
22	13:02	14:15	74	118.45	7:30	WNW – 8.7	78	252	66	259	3.63	33.2/25.1	31.54
23	13:20	15:31	132	107.28	6:30	WNW – 4.78	78	254	48	259	6.55	33.9/24.9	29.8
24	13:55	16:22	148	101.84	3:10	W – 3.48	70	259	36	258	6.34	34.9/26.4	29.9
25	14:39	17:01	143	102.82	8:15	SSE – 6.19	60	261	27	257	4.95	32.3/25.4	29.46
26	15:32	17:31	120	109.38	11:40	SSE – 14.15	48	260	20	256	2.97	33.4/24.4	29.5
27	16:43	17:45	63	119.52	11:40	SE – 9.63	31	258	16	255	0.68	33.8/25.7	31.1
28	Not exposed			130.71 at 17:59	12:05	W – 4.45			13	255		34.4/25.6	31.1
	Total		**680**						**Cumulative**		**25.12**	**Mean max 33.62**	**Mean 30.29**
February 1929													
6-10 shallow period when reef does not uncover but minimum dept over reef flat drops to around 5 cm in mid afternoons													
19	Not exposed			127.95 at 13:03	9:54	WNW – 1.99			82	310		35.2/27	30.36
20	12:45	14:35	111	112.98	2:20	NNW – 1.29	84	337	60	277	6.94	32.7/27	30.02
21	13:04	15:26	143	103.48	5:00	SE – 5.55	81	310	48	273	8.29	31.4/23.7	29.72
22	13:36	16:01	146	99.94	10:30	WNW – 5.86	74	291	37	270	7.73	33.9/25.8	30.28
23	14:14	16:30	137	102.03	9:10	NW – 2.97	65	283	32	269	6.43	34.9/23.9	29.72
24	14:58	16:53	116	108.67	0:00	S – 4.07	54	277	27	268	4.65	26.6/24.4	29.4
25	15:55	17:03	69	118.35	0:20	SW – 11.72	41	272	24	268	2.24	28.5/23.6	28
26	Not exposed			129.4 at 17:02	1:05	ENE – 22.03			24	268		29.5/23.6	29.6
	Total		**722**						**Cumulative**		**36.28**	**Mean max 31.59**	**Mean 29.64**

Table S1. Periods of predicted daytime low tide exposure of the coral platform in the Western Moat (datum level 122.8 cm relative to tide gauge zero). Timings predicted at 1 min intervals. Sunshine hours, wind speed (24hr mean) and direction, and air temperature from Orr (1933a). Water temperature in the Low Isles Anchorage from Moorhouse (1933). For details of the computation of insolation see Main Paper text.

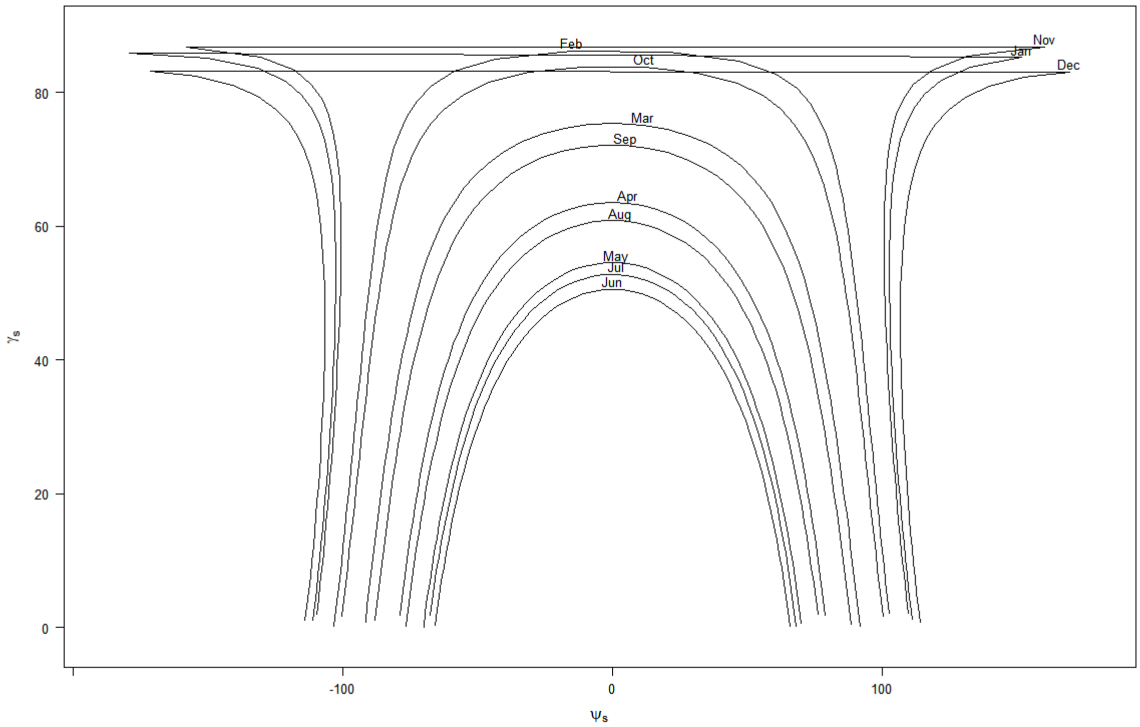

Fig S1. Annual sun altitude (y-axis) and azimuth (x-axis) plot for Low Isles. During the months of November-January the sun is in the southern hemisphere relative to the latitude of Low Isles, hence the shape of the plots for these months where the sun azimuth moves from east to west through due South (180^{o}) at midday.

Note on Sunshine Hours and Day Lengths

The instrument used by the Expedition to record sunshine hours would have been a Campbell-Stokes recorder [deduced from Plate V in Yonge (1930)] although this is not explicitly stated in Orr (1933b). This instrument burns a sun trace on a card when solar irradiance exceeds a threshold of 120 Watts m^{-2} (Horseman et al. 2013). On a typical clear sky day in austral summer, such as on 26 December 1998 at Cairns Airport, solar irradiance is less than this threshold during the initial 1 hour after sunrise and 1 hour before sunset. Thus, the effective day length for the purpose of comparing with the sun hour record is approximately 11 hours.

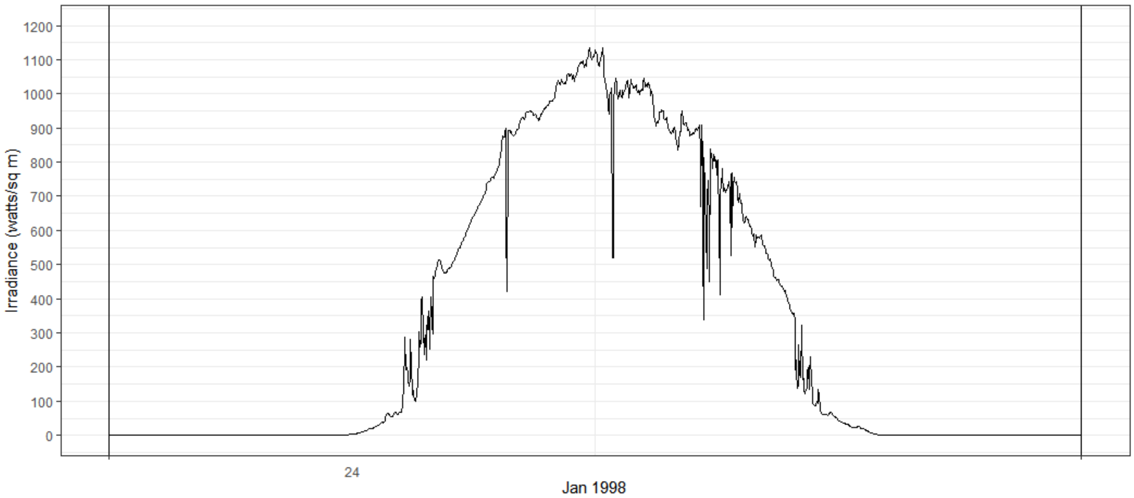

Fig S2. 24 Jan 1998 choice of clear sky day from Cairns 1998 data. 27.26 MJoules m^{-2}

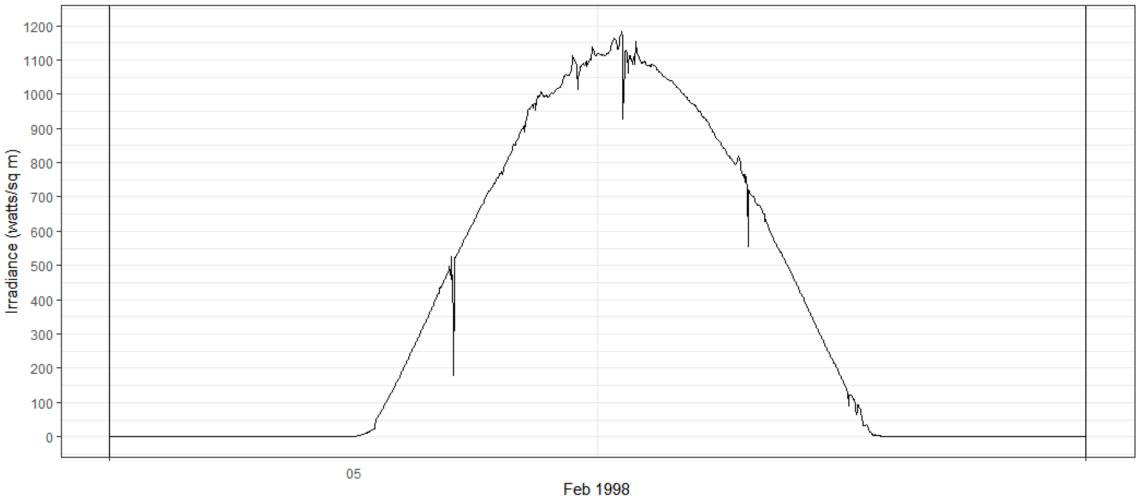

Fig S3. 5 Feb 1998 choice of clear sky day from Cairns 1998 data. 30.27 MJoules m^{-2}

Fig S4. 21 May 1998 choice of clear sky day from Cairns 1998 data. 20.21 MJoules m^{-2}.

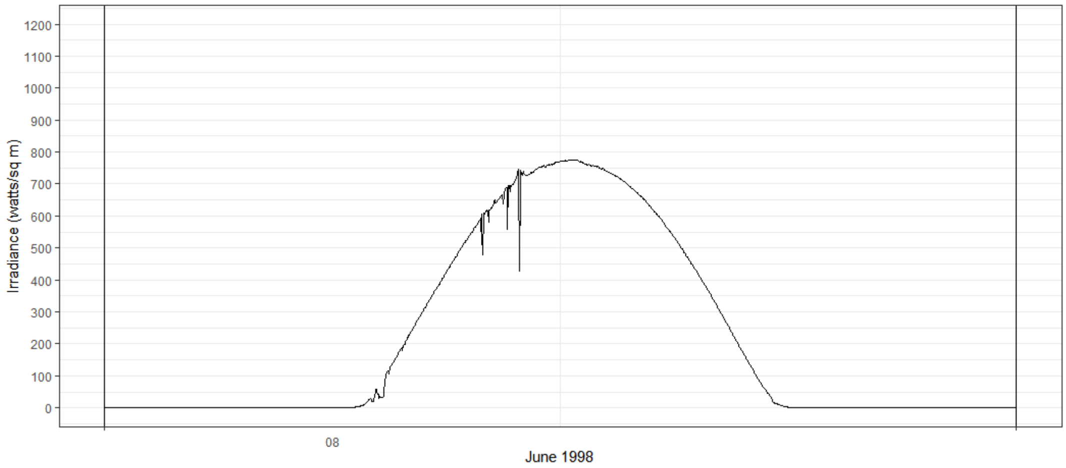

Fig S5. 8 June 1998 choice of clear sky day from Cairns 1998 data. 18.7 MJoules m^{-2}

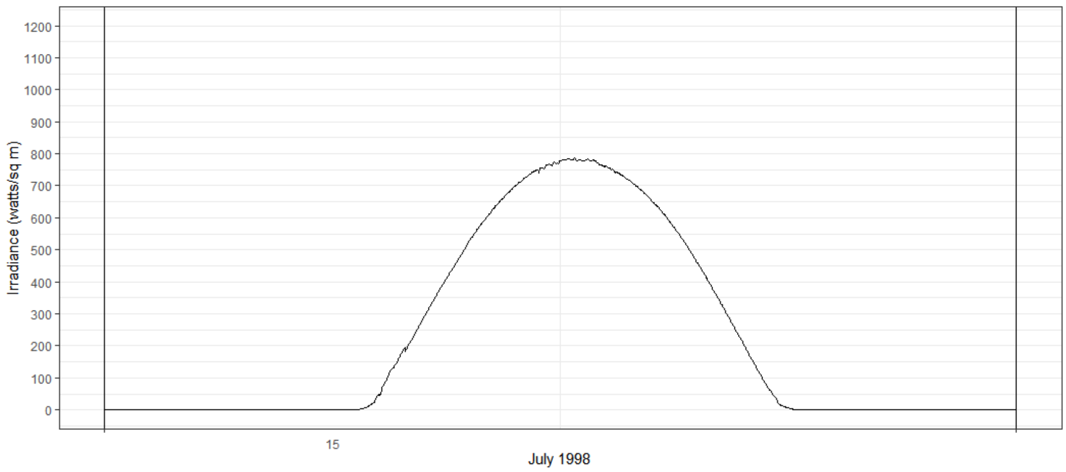

Fig S6. 15 July 1998 choice of clear sky day from Cairns 1998 data. 19.15 MJoules m^{-2}

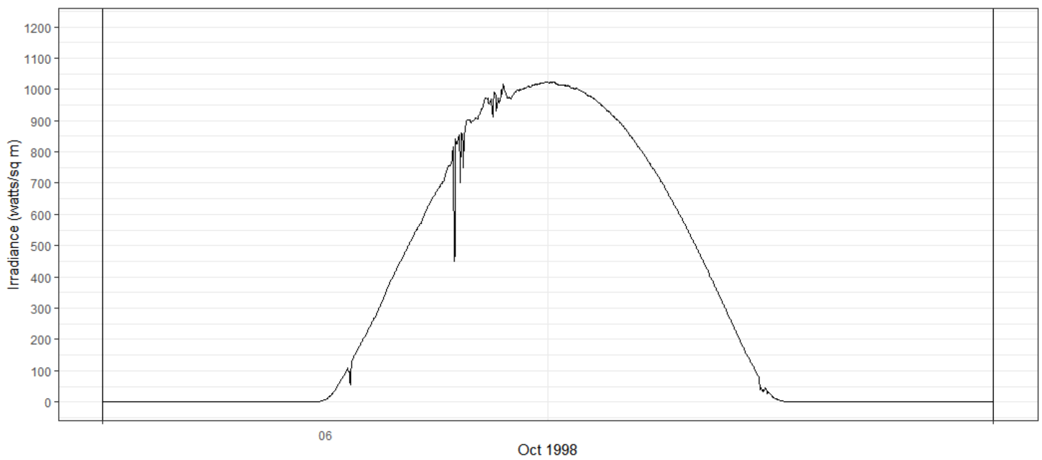

Fig S7. 6 Oct 1998 choice of clear sky day from Cairns 1998 data. 27.25 MJoules m^{-2}

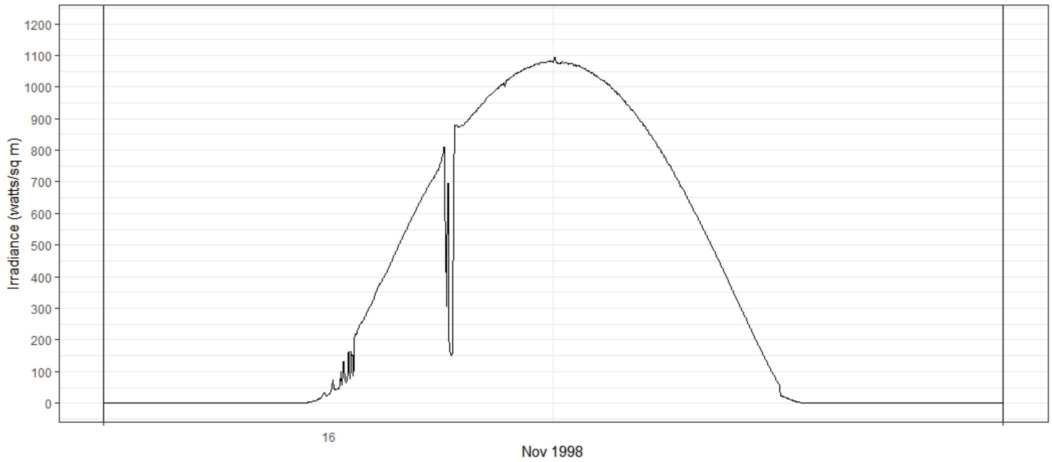

Fig S8. 16 Nov 1998 choice of clear sky day from Cairns 1998 data. 29.56 MJoules m^{-2}

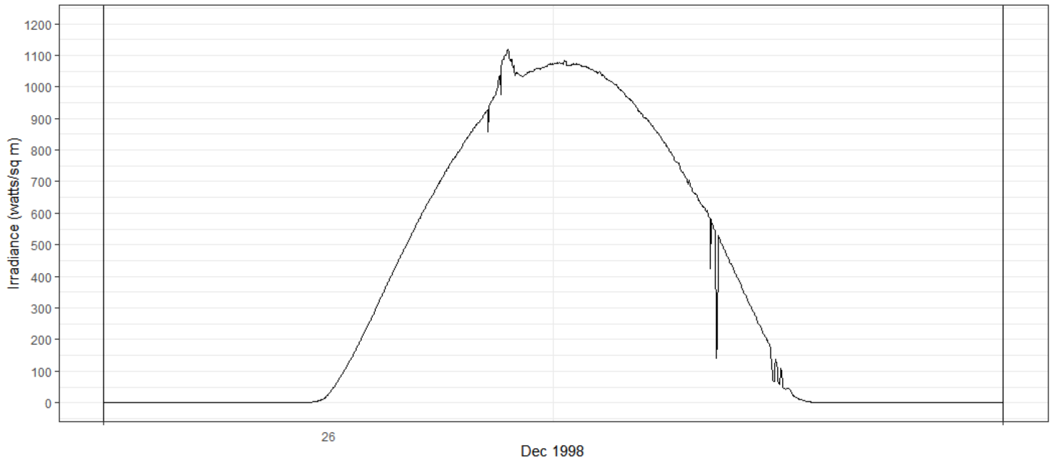

Fig S9. 26 Dec 1998 choice of clear sky day from Cairns 1998 data. 30.16 MJoules m^{-2}

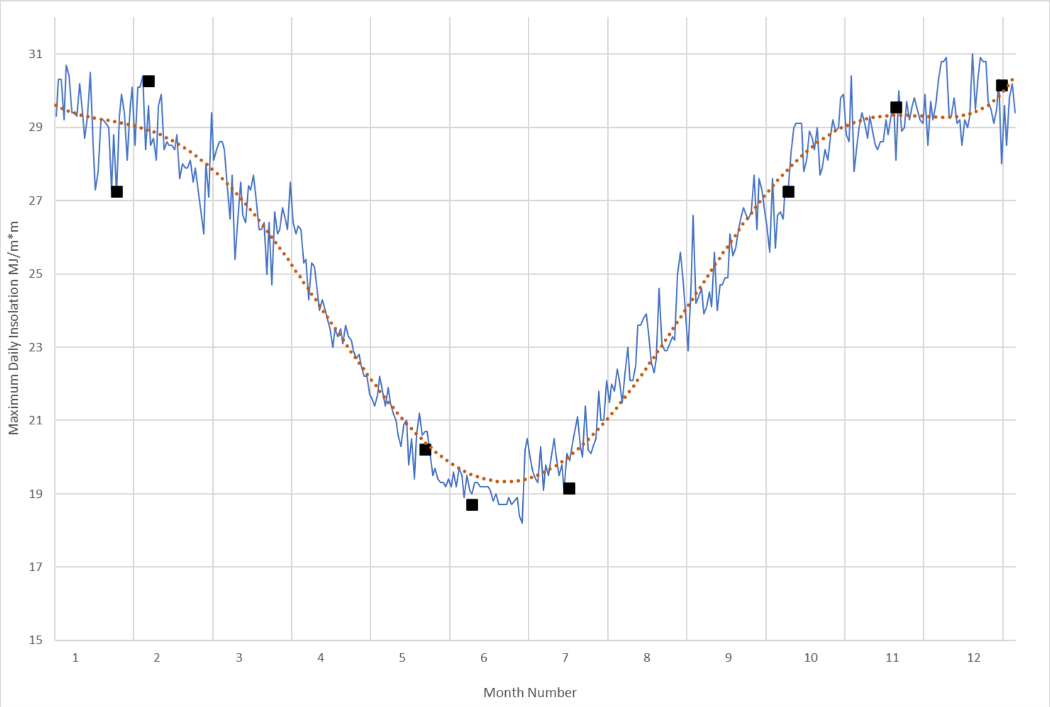

Fig S10. Maximum daily insolation 2007-2021 at Low Isles from satellite data. The brown dotted line is a 6th order polynomial fit to illustrate the seasonal variation. The black squares are the 'clear sky day' insolation from the Cairns 1-minute irradiance dataset, plotted for comparison (see Figs S2-9).

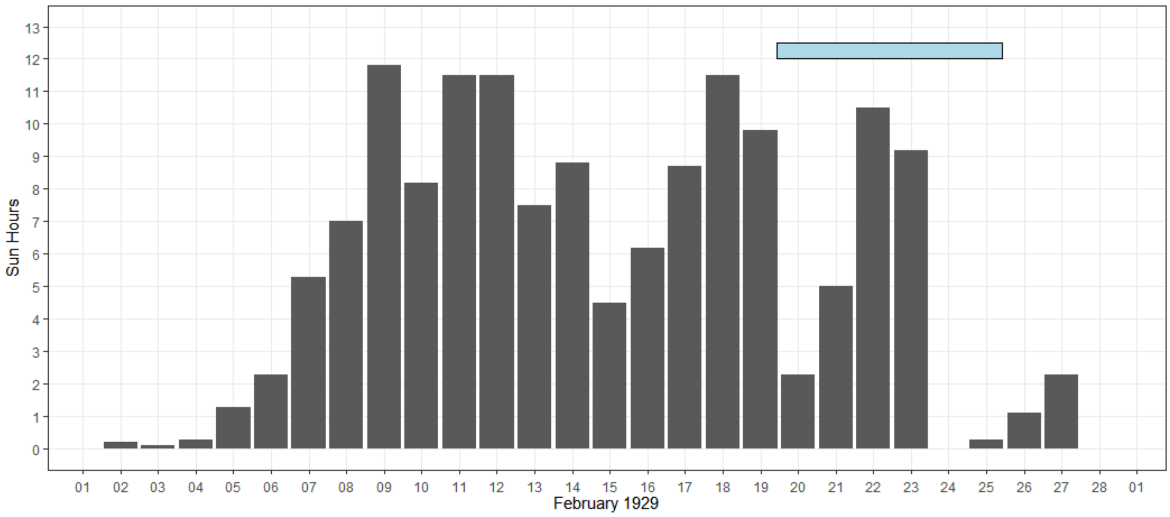

Fig S11. Daily sunshine hours February 1929. The horizontal blue bar indicates when daytime low tide exposure occurred on the Western Moat coral platform.

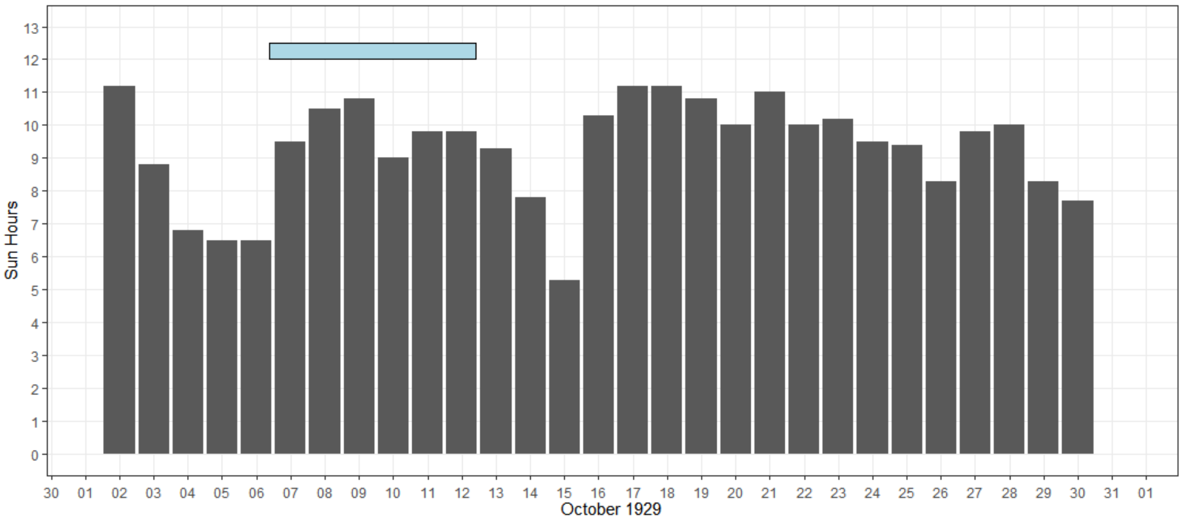

Fig S12. Daily sunshine hours October 1928. The horizontal blue bar indicates when daytime low tide exposure occurred on the Western Moat coral platform.

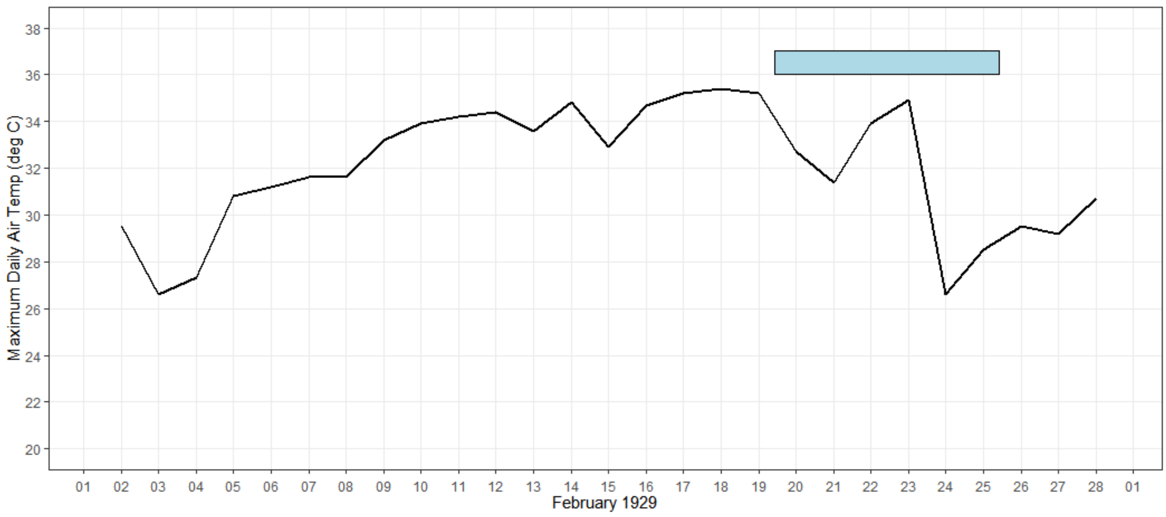

Fig S13. Air temperature (maximum daily °C) at Low Isles February 1929. The horizontal blue bar indicates when daytime low tide exposure occurred on the Western Moat coral platform.

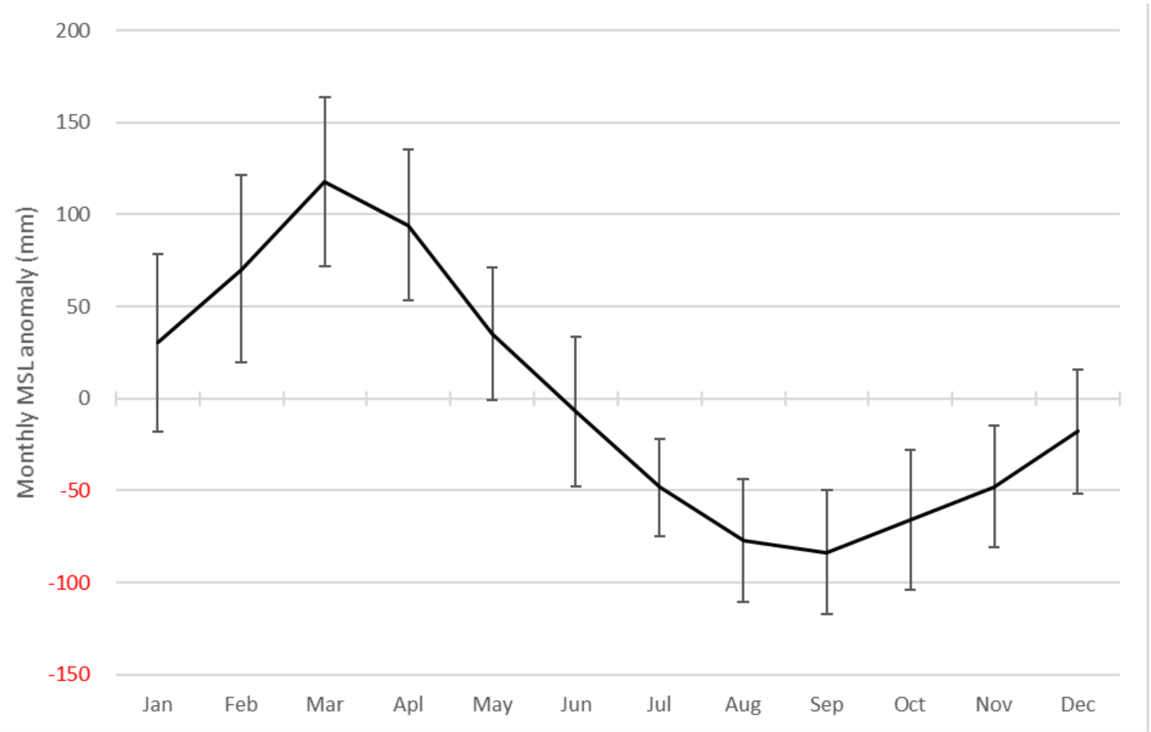

Fig S14. Seasonal variation in monthly mean sea level (MSL) (± standard deviation) at Cairns 1966-2019. Years with 12 months of data only (N = 44).

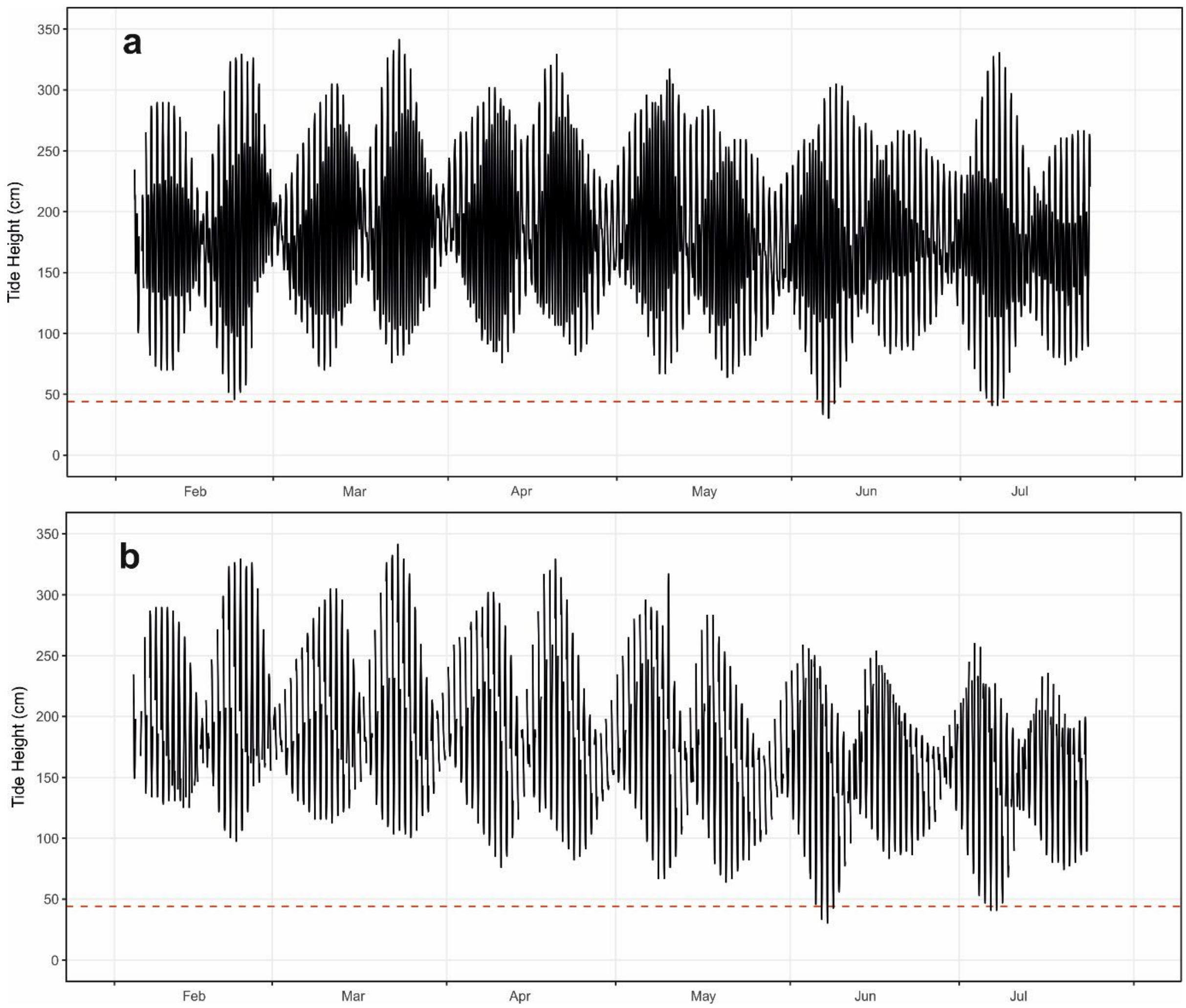

Fig S15. **a.** Low Isles tide gauge record (not predictions) 4 February-24 July 1929. **b.** Daytime (06:00-18:00) tides only plotted. The dashed red line is the uncovering height (44cm above TGZ) of the *Acropora spp.* zone on Traverse MS2 (Manton and Stephenson 1935).

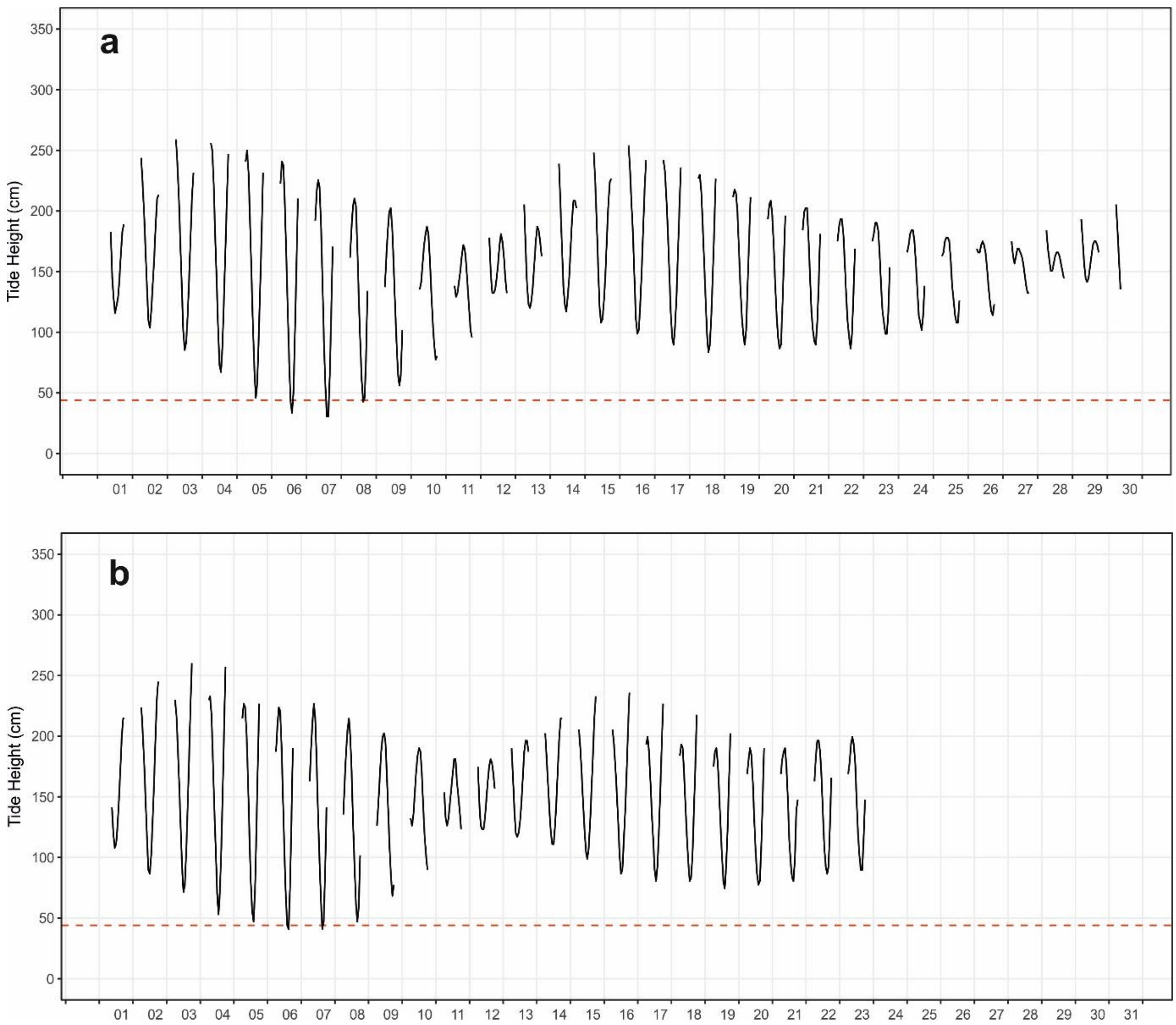

Fig S16. a. Low Isles tide gauge record (not predictions) June 1929. **b.** July 1929. Daytime (06:00-18:00) tides only plotted. The dashed red line is the uncovering height (44cm) of the *Acropora spp.* zone on Traverse MS2 (Manton and Stephenson 1935).

Date	Start time	End time	Minutes exposed	Minimum tide height (cm)	Sun (hrs:mins)	Wind direction & average speed (mph)	Sun at start time		Sun at end time		Max Insolation during low tide period	Air Temperature Max/Min	Anchorage surface water temp (17:30)
							Altitude (deg)	Azimuth (deg)	Altitude	Azimuth	MJoules m^{-2}	ºC	ºC
June 1929													
6	12:58	14:34	97	33.53	10:00	SW 6.85	49.8	346.4	39	319	4.02	27.6/22.0	24.1
7	13:27	15:24	118	30.48	10:00	SE 8.31	47.5	337	30.4	310	4.32	27.8/20.8	24.36
8	14:56	15:26	31	42.67	6:45	SSE 12.39	35.3	315	30	309	0.93	28.3/22.6	24.22
July 1929													
6	14:00	15:05	66	40.84	8:30	SE 12.4	44.7	323	35	314	2.51	25.5/19.7	21.84
7	14:53	15:31	39	40.84	5:00	SSE 19.21	37.1	316	30.4	309	1.25	24.6/19.9	21.7

Table S2. Periods of aerial exposure for the Anchorage Reef (datum level 44 cm relative to tide gauge zero). Sunshine hours, wind speed (24hr mean) and direction, and air temperature from Orr (1933a). Water temperature in the Low Isles Anchorage from Moorhouse (1933). For details of the computation of insolation see Main Paper text.

Notes on the 1929 Low Isles Tide Gauge

The importance of determining 'changes of level' was outlined by Frank Debenham in his Memorandum of work to be carried out by the Royal Geographical Society (RGS) members of the Barrier Reef Expedition of 14 March 1928; this highlighted the need to establish a '*drum-recording tide gauge of a portable type*' at Low Isles to acquire a year's record of water level variations. Debenham was of the view that '*these records when reduced should give a figure for M.S.L.* [Mean Sea Level] *at Low Islands of considerable precision*'[1]. The tide gauge came to be under the supervision of Michael Spender, a member of the Expedition's 'Geographical Section'.

A suitable tide gauge was duly acquired and shipped to Australia; the full details of the instrumentation are described in Spender (1932). Unfortunately, however, the delivery of the tide gauge to Low Isles was considerably delayed by a shipping strike at the start of the Expedition [2] and the equipment did not arrive at Low Isles until 24 November 1928 [3].

Following scoping of an appropriate non-drying site on the margins of the Anchorage (Fig S17), four poles of *Rhizophora* mangrove were obtained from the mouth of the Daintree River on the mainland on 15 January 1929 [4]. The erection of the poles in a tripod to take the tide gauge began at 2 a.m. on 26 January 1929 [5]. After some difficulties with erecting the supporting structure (see Spender 1932), the gauge became operational on 8 February 1929, with hourly water level records until 24 July 1929 (Figs S18 & S19). There was only one break in recording, of 24 hours between 4 and 5 May 1929.

On return from the Expedition, on 30 October 1929, the Secretary to RGS, Arthur Hinks, wrote to Spender [6] to inform him that the record had been sent to Arthur Doodson, at the Liverpool Observatory and Tidal Institute, asking for a full analysis [7] by 16 December 1929 (as Spender was giving a lecture at the RGS that evening) [8].

The analysis was, however, delayed; following some pressure from Spender [9], Joseph Proudman wrote to Hinks on 12 April 1930, saying that the analysis would be complete by end

[1] F Debenham, Memorandum of work to be carried out by the R.G.S. members of the Barrier Reef Expedition, RGS Correspondence Block CB9 Great Barrier Reef 1921-30, in file 2.
[2] JA Steers, Great Barrier Reef Expedition: Geographical Section, Report of work Aug – Nov. 1928, RGS Correspondence Block CB9 Great Barrier Reef 1921-30, in file 3.
[3] British Museum (Natural History). Papers of Sir Maurice Yonge. Subseries B3. Great Barrier Reef Expedition, 26 May 1928-17 May 1929. Journal kept by M.J. Yonge and others, 26 May 1928-5 August 1929 (AJCP ref: http://nla.gov.au/ nla.obj-2374648493).
[4] British Museum (Natural History). Papers of Sir Maurice Yonge. Subseries B3. Great Barrier Reef Expedition, 26 May 1928-17 May 1929. Journal kept by M.J. Yonge and others, 26 May 1928-5 August 1929 (AJCP ref: http://nla.gov.au/ nla.obj-2374650178).
[5] British Museum (Natural History). Papers of Sir Maurice Yonge. Subseries B3. Great Barrier Reef Expedition, 26 May 1928-17 May 1929. Journal kept by M.J. Yonge and others, 26 May 1928-5 August 1929 (AJCP ref: http://nla.gov.au/nla.obj-2374650437).
[6] Hinks to Spender, 30 October 1929; Royal Geographical Society CB9 1921-30, filed under Spender.
[7] A note at the end of Spender's 1932 paper says '[Note by Editor G.J. We must not omit our thanks to the Director of the Liverpool Tidal Institute, who very kindly undertook to compute at his Institute for a modest fee the tidal observations made by the Great Barrier Reef Expedition, and to deduce the constants published above.]'. The 'Editor G.J.' was Hinks.
[8] Spender to Hinks, agreeing to read his paper on 16 December, 18 October 1929; Royal Geographical Society CB9 1921-30, filed under Spender. This paper was subsequently published as: Spender, M. 1930. Island-reefs of the Queensland Coast. *The Geographical Journal* 76, 193-214, 273-293.
[9] Spender to Hinks, 3 April 1930; Royal Geographical Society CB9 1921-30, filed under Spender.

April 1930 [10]. The report was supplied on 28 April 1930 with Hinks thanking Doodson on 1 May 1930 [11]. It is this report, and the transcribed datasheets, that have recently been found at the British Oceanographic Data Centre (BODC). The tidal paper itself had a rather long gestation [12] but was finally submitted to The Geographical Journal on 22 September 1931 [13].

In the context of the present study, one potential complication with the 1929 tide gauge data set is that the time zone used to record the measurements was not initially clear. However, we were able to verify this from several sources including other records of the Expedition and also from later data from almost the same location recorded by the Queensland Department of Transport between 21 January and 23 February 1983. Harmonic constants from this later data set are included in the current Australian Tide Tables. They are very similar to those derived from the 1929 data by both Doodson and us. They confirm the general quality of the 1929 data as regards its tidal content. They also confirm that the 1929 data were recorded in time zone UTC+10 hours.

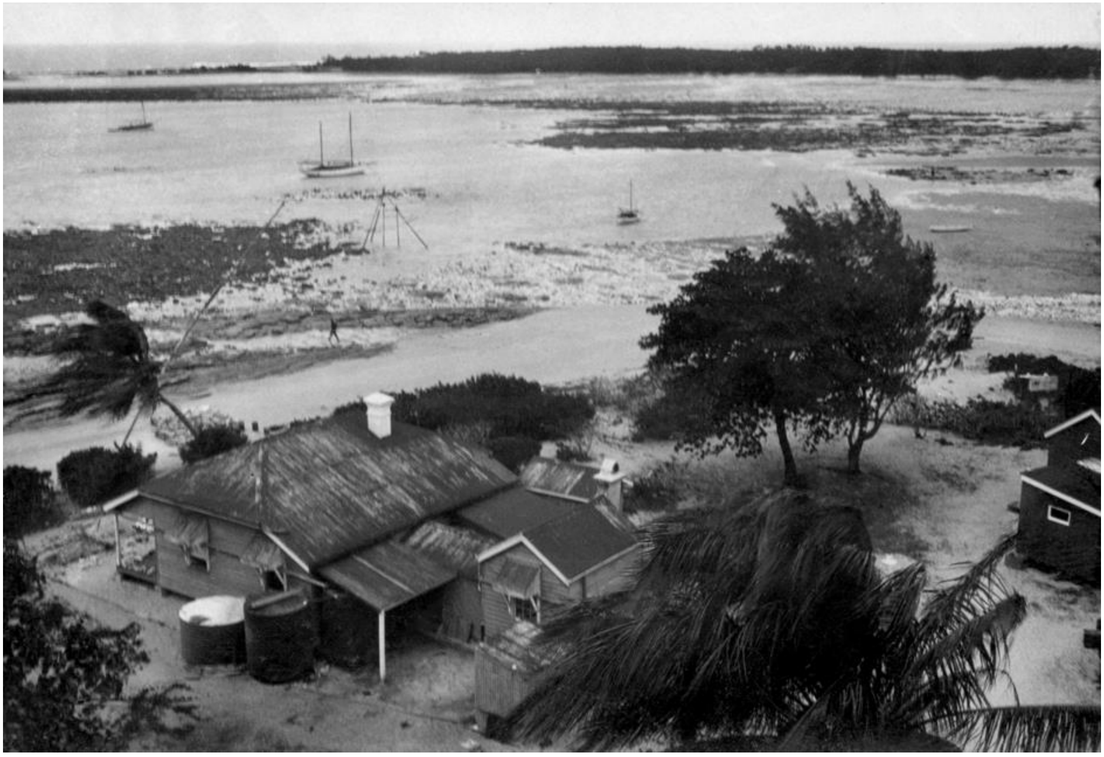

Fig S17. The tide gauge tripod on the western margin of the Anchorage, Low Isles, seen below Expedition yacht 'Luana', the location for Moorhouse's (1933) twice daily temperature measurements (photographer unknown, by kind permission of the Royal Geographical Society (with IBG)).

[10] Proudman to Hinks, 12 April 1930; Royal Geographical Society CB9 1921-30, filed under Spender.
[11] As noted in Spender's 1930 paper. And Hinks to Doodson, 1 May 1930; Royal Geographical Society CB9 1921-30, filed under Spender.
[12] 'It is high time we published that paper of yours. I am getting rather afraid that if you are in workshops at 6 a.m. you are not likely to be very fresh in the evenings to completely re-write the paper, as Stanley Gardiner wanted you to'. Hinks to Spender, 23 May 1930; Royal Geographical Society CB9 1921-30, filed under Spender. The correspondence with Stanley Gardiner has not been traced. Spender replied to Hinks on 25 May 1930 to say that he would 'make a few adjustments' Royal Geographical Society CB9 1921-30, filed under Spender.
[13] paper submission noted in Royal Geographical Society CB10, 1931-40, filed under Spender.

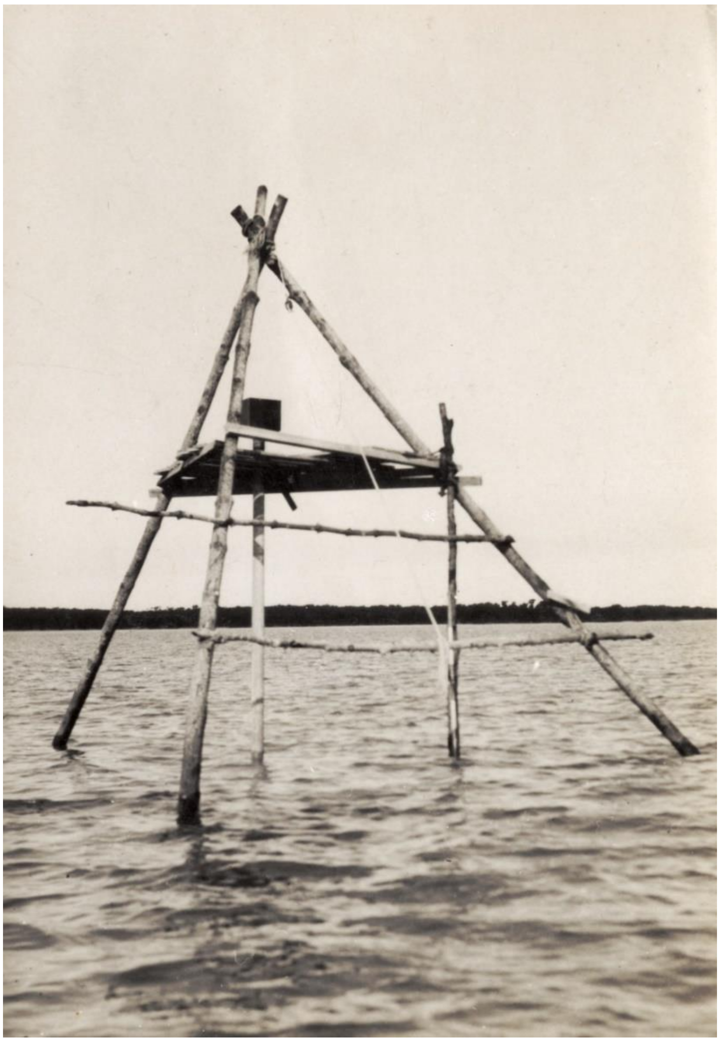

Fig S18. Staging, gauge and 'tick-pole' at half-tide stage (photo: M Spender, by kind permission of the Royal Geographical Society (with IBG)).

Fig S19. Tide Gauge in position and recording (photo: M Spender, by kind permission of the Royal Geographical Society (with IBG)).

Notes on the position of the Mattie Yonge ('MY') photograph (Main Paper Fig 9).

The MY photograph (Fig S21) can be compared with one taken from near the red cross on Fig 1 (Main Paper) which is adjacent to the 'Tripnuestes Spit' (Fig S20). Both photographs show (1) the same alignment of features (including the tide gauge tripod, position and view of lighthouse, details of trees) on Low Isles sand cay (2) the mainland coastal hills in the background (although this is washed out in the poor quality MY photo but can just be discerned) (3) and a broad extent of open water (the Anchorage) between the foreground and Low Isles.

Fig S20. The sand cay at Low Isles at the time of the Expedition (1928-9) from Tripnuestes Spit looking across the Anchorage (from **Fig 3a** in Spencer et al. (2021)). The black arrow points to tide gauge tripod. The red lozenge highlights three objects on the shoreline. In the background are the range of hills on the mainland

Fig S21. (**Fig 9 Main Paper).** The eastern reef edge of the Anchorage looking WSW towards the Low Isles sand cay. The tide gauge 'tripod' is just visible (arrowed).

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