

Large amplitude, leaky, island-generated, internal waves around Palau, Micronesia

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Abstract

Three years of temperature data along two transects extending to 90 m depth, at Palau, Micronesia, show twice-a-day thermocline vertical displacements of commonly 50–100 m, and on one occasion 270 m. The internal wave occurred at a number of frequencies. There were a number of spectral peaks at diurnal and semi-diurnal frequencies, as well as intermediate and sub-inertial frequencies, less so at the inertial frequency. At Palau the waves generally did not travel around the island because there was no coherence between internal waves on either side of the island. The internal waves at a site 30 km offshore were out-of-phase with those on the island slopes, suggesting that the waves were generated on the island slope and then radiated away. Palau Island was thus a source of internal wave energy for the surrounding ocean. A numerical model suggests that the tidal and low-frequency currents flowing around the island form internal waves with maximum wave amplitude on the island slope and that these waves radiate away from the island. The model also suggests that the headland at the southern tip of Palau prevents the internal waves to rotate around the island. The large temperature fluctuations (commonly daily fluctuations ≈ 10 °C, peaking at 20 °C) appear responsible for generating a thermal stress responsible for a biologically depauperate biological community on the island slopes at depths between 60 and 120 m depth.

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1. Introduction

The surface waters of oceanic islands and atolls in the tropical Pacific and Indian oceans are oligotrophic, yet they support rich coral reefs and fisheries. Coral reefs are tropical marine environments usually found in the upper 60 m, which are generally considered thermally stable environments. There are nutrients tantalisingly close in deeper water (Rougerie et al., 1992). There is considerable interest in understanding and quantifying the mechanisms that cause upwelling of these deeper waters into the zone of coral reef growth. Island-generated

oceanographic processes may locally lift these nutrients to near the surface. These processes include isotherm doming in island wakes in the presence of strong ($>0.5 \text{ m s}^{-1}$) currents (Hogg, 1972; Hogg et al., 1978; Gordon and Hughes, 1981; Wolanski, 1986; Heywood et al., 1990). Such strong currents are uncommon. Boundary mixing may also result in nutrient enrichment at the thermocline level (Simpson et al., 1982; Simpson and Tett, 1986; Heywood et al., 1990; Franks, 1992). However, this mixing occurs typically at 100 m depth, and it is unclear how these nutrients would reach the coral reefs located at 40 m depth and shallower. Geothermal endo-upwelling within the substrate may also provide nutrients to surface waters (Rougerie et al., 1992), but the supporting data are lacking. In the presence of strong tidal currents in passages through

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reefs, a Bernoulli-like local upwelling effect may also locally lift the nutrients, though this seems to favour the bottom-dwelling *Halimeda* calcareous algae and not the coral reefs (Wolanski et al., 1988). Island-generated, internal waves may also exist and generate localised upwelling events. Such waves were first noticed around Bermuda (Wunsch, 1972) in deep water (> 272 m depth). These waves have since been reported in surface waters near Mururoa atoll, French Polynesia (Rancher and Theau, 1988), near Tahiti, French Polynesia (Wolanski and Delesalle, 1995), and near Scott Reef, on the slope of Australia's northwestern continental shelf (Wolanski and Deleersnijder, 1998). Numerical models suggest that these internal waves are island-generated, with highest wave amplitude on the island slope, that the waves are leaky as energy is radiated away from the island, they occur predominantly at tidal frequencies, and they may rotate around a topographically smooth island (Garrigues et al., 1993; Wolanski and Delesalle, 1995; Wolanski et al., 2003).

We present additional evidence of the existence of these internal waves, measured with bottom-mounted thermographs over three years, around Palau, Micronesia ($7^{\circ}20' \text{ N}$, $134^{\circ}22' \text{ E}$; Fig. 1). Mixed semi-diurnal, 2-m tides prevailed. The internal waves were most pronounced during spring tides, with typical amplitude of 50–100 m, peaking at 270 m, and were distributed broadly over a wide range of diurnal and semi-diurnal frequencies not restricted to the tidal frequencies. These waves were leaky and were observed 30 km from the island. By merging field and numerical model studies, we suggest that the salient bathymetry comprising headlands and canyons prevents the waves from rotating around the island. This generates flow instabilities resulting in some cases in enhanced leakage of internal waves from headlands, and occasionally in the internal wave transforming in an internal bore running up the slope of the island coral reef depths. However, below the reefs at roughly 60–120 m, thermal change is on occasion large and rapid (up to 20° C in 30 min). More frequently temperature changes of 8–10 $^{\circ} \text{ C}$ in typically an hour occur at these depths, making this a thermally dynamic, potentially stressful environment. Any benthic organisms living there must either be adapted to tolerate these temperature swings, or be able to change depth rapidly to stay at a favourable temperature level. Qualitatively it has been observed that the zone below coral reefs in Palau is biologically depauperate and has relatively low biomass of benthic organisms. There is a biological community occurring at these depths, identifiable by the occurrence of certain species, and the members of this community must represent extremely thermally hardy species. Temperature changes may also be the factor that controls the lower limit of the distribution of coral reefs in Palau, rather than another factor such as light penetration.

2. Methods

2.1. Field data

The main Palau Island reef tract (Fig. 1) is a single platform about 150×40 km in size with deep ocean (depth > 3000 m) on all sides. Depth > 100 m is found no further than 500 m from the reef front.

Long-term, water temperature monitoring stations were established at three depths (15, 55 and 90 m) along two transects, the Sharp Drop-Off transect (SDO; $7^{\circ}16.418' \text{ N}$; $134^{\circ}31.440' \text{ E}$) transect (Fig. 1) in mid-1999 and the Ulong transect (UL; $7^{\circ}17.453' \text{ N}$; $134^{\circ}14.442' \text{ E}$) in mid-2001. In addition, additional monitoring stations were established at 2, 35 and 75 m depth on the SDO transect in early 2000. Onset Hobo Pro-8 recording thermographs (precision 0.01° C) were installed in pressure-proof housings and recorded at 30-min intervals. A thermistor on a cable was installed against a metal plate exposed to outside water temperature. A second channel recorded temperature from an internal thermistor. As long as water temperatures did not change rapidly (less than 2° C in 30 min), the internal and external thermistor records matched. When there were large temperature swings (8–10 $^{\circ} \text{ C}$ in 30 min) the internal thermistor lagged about 30 min behind the external. The internal thermistor was often used to confirm external readings (where large temperature changes were involved) to alleviate any doubt of sensor error. The thermographs were calibrated using NIST traceable mercury thermometers accurate to 0.01° C . The waterproof external thermistors were immersed in a circulating water baths whose mercury thermometer temperature was recorded at 1-min intervals. Calibrations were performed both pre- and post deployment. Correction factors for all instruments were derived and temperature data are considered to be accurate within 0.1° C based on these calibrations.

Thermographs were deployed using scuba diving techniques, the deeper units (75 and 90 m) requiring use of mixed-gas diving techniques. Instruments were usually recovered, downloaded, recalibrated and redeployed, within 1–2 days of retrieval.

To demonstrate the leakage of internal waves to the surrounding ocean, a single thermograph recording at 5-min intervals was installed during the period 4–7 December, 2002 at 90 m depth from a fish attracting device (FAD) located at $7^{\circ}14.8' \text{ N}$; $134^{\circ}44.7' \text{ E}$, about 30 km east of Palau, over a water depth of about 3000 m (Fig. 1). The FAD had a surface float moored to an anchor on the bottom by several thousands of metres of line. During the same period a second thermograph sampling at a 5-min interval was installed at the SDO site, also at 90 m depth, to provide direct comparison of temperatures at the two sites. An ADCP was suspended beneath a 10-m vessel moored at the FAD float for 24 h

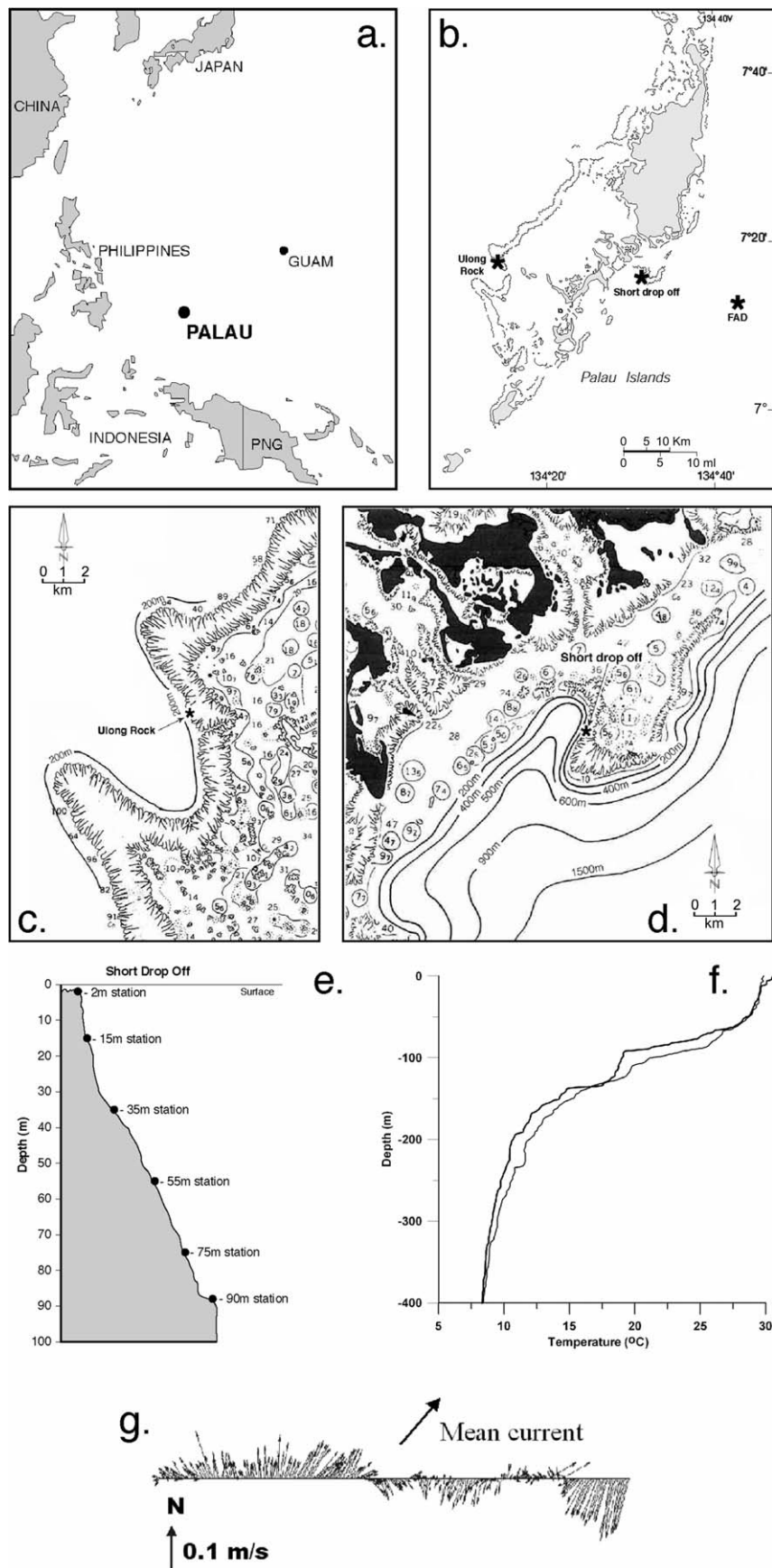


Fig. 1. (a,b) General location maps. (c,d) Bathymetry around the Ulong Rock (UL) and Sharp Drop Off (SDO) transects. (e) Vertically undistorted seafloor profile at the SDO transect. (f) Two CTD casts near Palau (adapted from Hata et al., 1998). (g) Time-series plot of mean current and the tidal currents in the top 20 m of the water column on 6–7 December, 2002, starting and finishing at 12:00 h, at the FAD site.

(6–7 December, 2002) to determine the surface currents in the open ocean east of Palau.

Hourly water levels at Koror (see a location map in Fig. 1) during the study period (1999–2002) were provided by NOAA.

Storm data during the period 1999–2002 that might have influenced Palau were collected. These are both tropical storms and typhoons. The start of the period was simply the time when the storm was building, while the end of the period was when it was decreasing.

Time series of the Southern Oscillation Index were provided by NOAA.

Two CTD profiles measured at the same site 10 km off Palau and extending to 400 m depth were provided by H. Kayanne.

2.2. Data processing

The coherence computations followed the procedure of Raupach and Mitchell (1977).

Low-frequency time series were obtained by applying the Godin (1972) moving average filter, $A^2_{24}A_{25}/24^225$.

2.2.1. Wavelet transform

The wavelet transform (WT) is used to study the time evolution of various scales present in the time series. WT optimises both time and frequency resolution to a maximum extent. This is done by choosing the best window width for a particular frequency band. Our wavelet analysis follows the methods of Daubechies (1992), Meyers et al. (1993), Foufoula-Georgiou and Kumar (1994), and Naithani et al. (2001, 2002, 2003). In brief, the wavelet transform is the convolution of the time series $f(t)$ and a set of functions $\Psi_{a,b}(t)$ called wavelets. WT is defined as:

$$Wf(a,b) = \frac{1}{\sqrt{a}} \int f(t) \Psi \left[\frac{t-b}{a} \right] dt$$

where a is the scaling parameter, b is the translation parameter and $\Psi(t)$ is the analysing wavelet. The later is dilated by the scale a and translated by length b to control the width (frequency) and the location of the window, respectively. The normalisation factor $1/\sqrt{a}$ is chosen so that variations with the same amplitude at different timescales would contribute equally to WT.

The Morlet wavelet, $\Psi(t) = \pi^{-1/4} \exp(-i\omega t) \exp(-t^2/2)$, was used. The application of this wavelet for various geophysical time series can be seen in Meyers et al. (1993), Foufoula-Georgiou and Kumar (1994), and Naithani et al. (2001, 2002, 2003).

2.3. Numerical modeling

The two-layer, non-linear numerical model of Wolanski et al. (2003) was implemented in a cylindrical model domain, with Palau at its centre, the outer radius of the

model domain was 200 km and the inner radius was 8 km. The outer boundary was open. The angular resolution was 2.5° . There were 46 grid points along a radial, which were unevenly spaced so that maximum resolution was achieved near the island. The buoyancy difference between the two layers, and the friction and eddy viscosity parameters were set to be the same as in Wolanski et al. (2003). The model was forced by a tidally-varying sea level gradient that was adjusted so as to reproduce the tidal currents observed at the FAD. A net sea-level gradient was also added in order to generate an uniform current in the far-field of the island. A sponge layer was added at the open boundary to prevent the reflection of outward-going internal waves back into the model domain.

3. Results

Generalised offshore bathymetry (Fig. 1c,d) near the two transects was taken from Defense Mapping Agency charts 81141 (Palau Islands) and 81151 (Arangel Channel and Koror Road). Direct diving observations at the sites indicate a steep profile (greater than $60\text{--}75^\circ$ slope) to 100–120 m depths. Fig. 1e shows the undistorted profile of the SDO transect site. Observations from a submersible at SDO indicate a steep slope below 120 m (roughly $45\text{--}60^\circ$) gradually decreasing as depth increases.

Fig. 1f shows two vertical profiles of temperature. The well-mixed, oligotrophic surface layer was about 70 m thick. The internal Rossby radius of deformation was about 15 km.

The stratification was strongest between 100 and 150 m. There were also maximum differences of 30 m in isotherm elevation between the two CTD casts, and these can be attributed to internal waves. The slope of the semi-diurnal internal tide rays, calculated following Baines (1982), is much smaller than the slope of the seafloor. This implies that internal tides propagating towards the island are reflected offshore.

Calm weather prevailed on December 6–7, 2002, when spring tides prevailed. During that time a mean northeastward surface current of speed of about 0.12 m s^{-1} was measured at the FAD mooring (Fig. 1g). At that site the tidal currents rotated clockwise with peak speed of about 0.12 m s^{-1} .

The Southern Oscillation Index (SOI) was about 10 from 1999 to mid-2000 and decreased to about -10 near the end of the sampling period (Fig. 2). The mean sea level and the low-frequency temperature at 90 m were highly correlated (see Fig. 2; $r^2 \approx 0.8$). Neither the mean sea level nor the low-frequency temperature at 90 m was correlated with the SOI ($r^2 < 0.3$).

Semi-diurnal, meso-tides prevailed, with a pronounced diurnal inequality, and a strong spring-neap cycle; the tidal range was about 2 m at spring tide and 1 m at neap tide (Fig. 2).

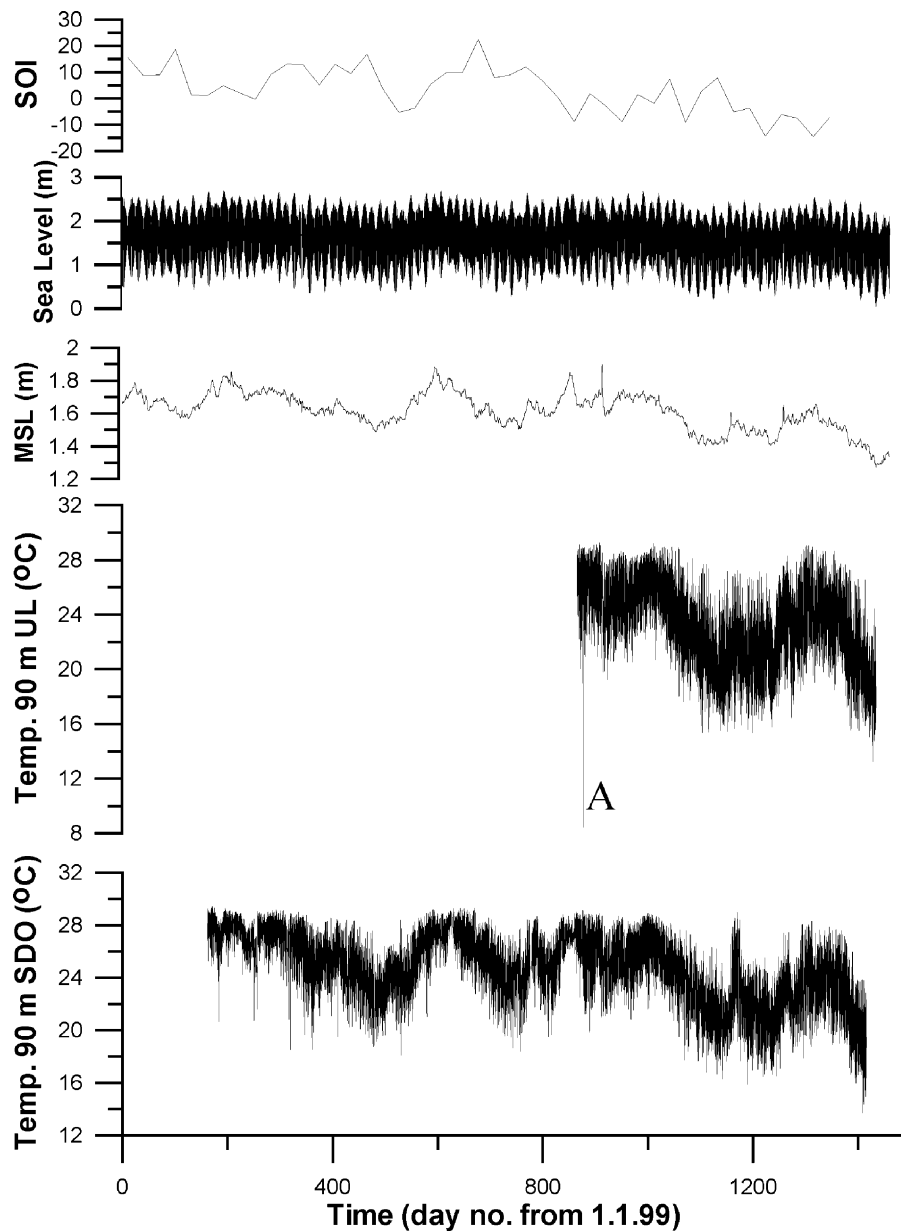


Fig. 2. Time-series plot of the Southern Oscillation Index (SOI), the sea level at Koror, the mean sea level (MSL) at Koror, and the water temperature at 90 m depth at UL and SDO. The event 'A' is discussed in the text.

There were large temperature variations (Fig. 2), implying vertical displacements of the isotherms. Details of some of these temperature fluctuations over a 1-day duration on 16 April, 2001 are shown in Fig. 3 for depth points along the SDO transect. The temperature at 2 m depth showed a weak (0.5°C) diurnal fluctuation, associated with heating in daytime and cooling at nighttime. At 15 m depth, a cold-water intrusion was experienced once, and at all other depths the cold-water intrusion was experienced twice. The maximum temperature fluctuation during that day was about 5°C . The internal waves thus lifted water upwards by about 40 m on that day. Beside the two semi-diurnal events

observed at all depths >15 m, there were also higher-mode waves, particularly in deeper waters.

There were 52 events in 2001–2002 when the temperature fluctuation at UL at 90 m depth was equal or greater than 8°C , implying a thermocline fluctuation of about 80 m. There were about 15 events when the thermocline fluctuation was equal or greater than 100 m. During the event marked A in Fig. 2, the thermocline fluctuation was 270 m and this lasted 1.5 h.

The temperature fluctuations at 90 m were about 30% greater at the UL than at the SDO transect.

The temperature fluctuations at SDO and the FAD mooring on 6–7 December, 2002, were primarily at

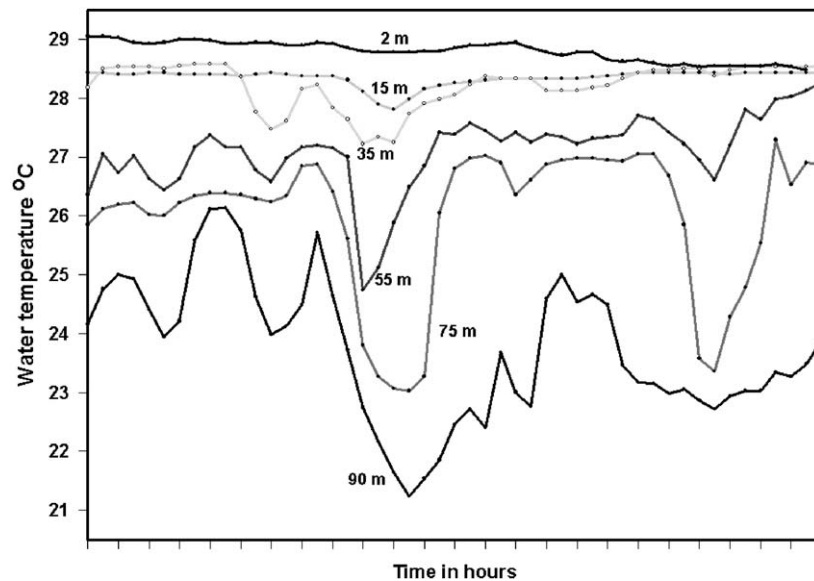


Fig. 3. Time-series plot during 16 April, 2001, starting and finishing at midnight, of the water temperature at six depths between 2 and 90 m at the SDO transect.

semi-diurnal frequency, they were of similar magnitude and about 90° out of phase (Fig. 4).

There was no significant coherence ($c_o^2 < 0.3$ for periods < 10 days; not shown) between the temperature time series at UL and SDO. At times the fluctuations

were in phase, and at other times they were out of phase on either side of Palau.

No significant coherence was found (not shown) between the Southern Oscillation Index and the water temperature at 90 m depth at UL or SDO.

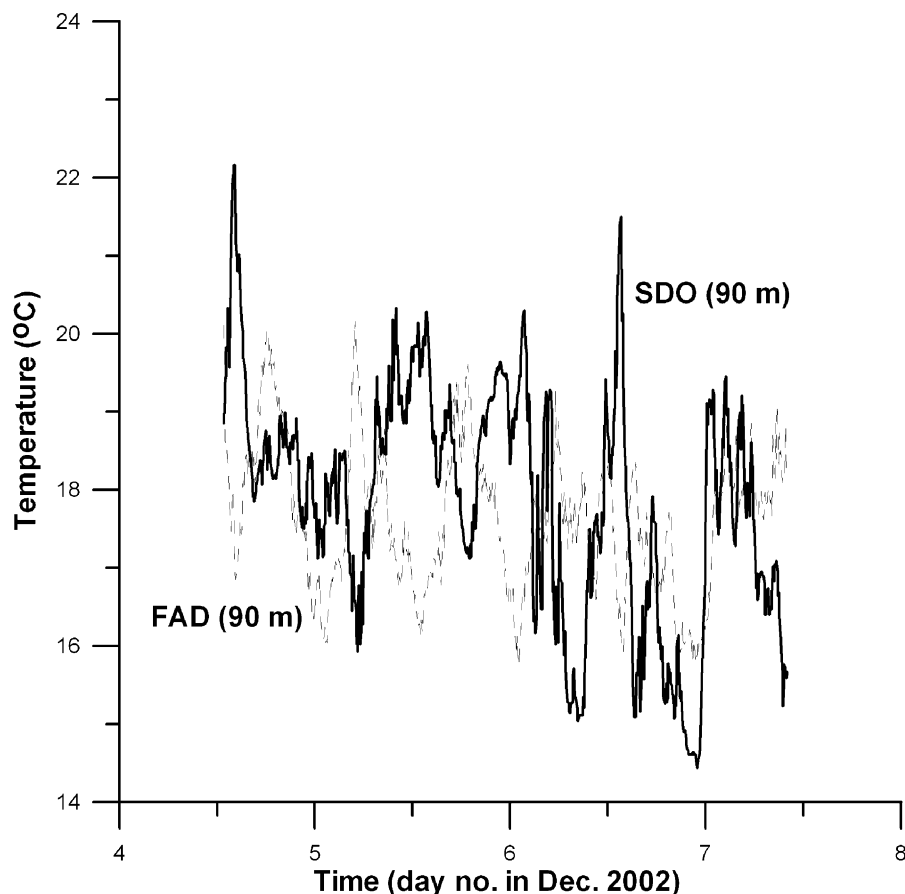


Fig. 4. Time-series plot of the water temperature at 90 m depth at the SDO and FAD sites.

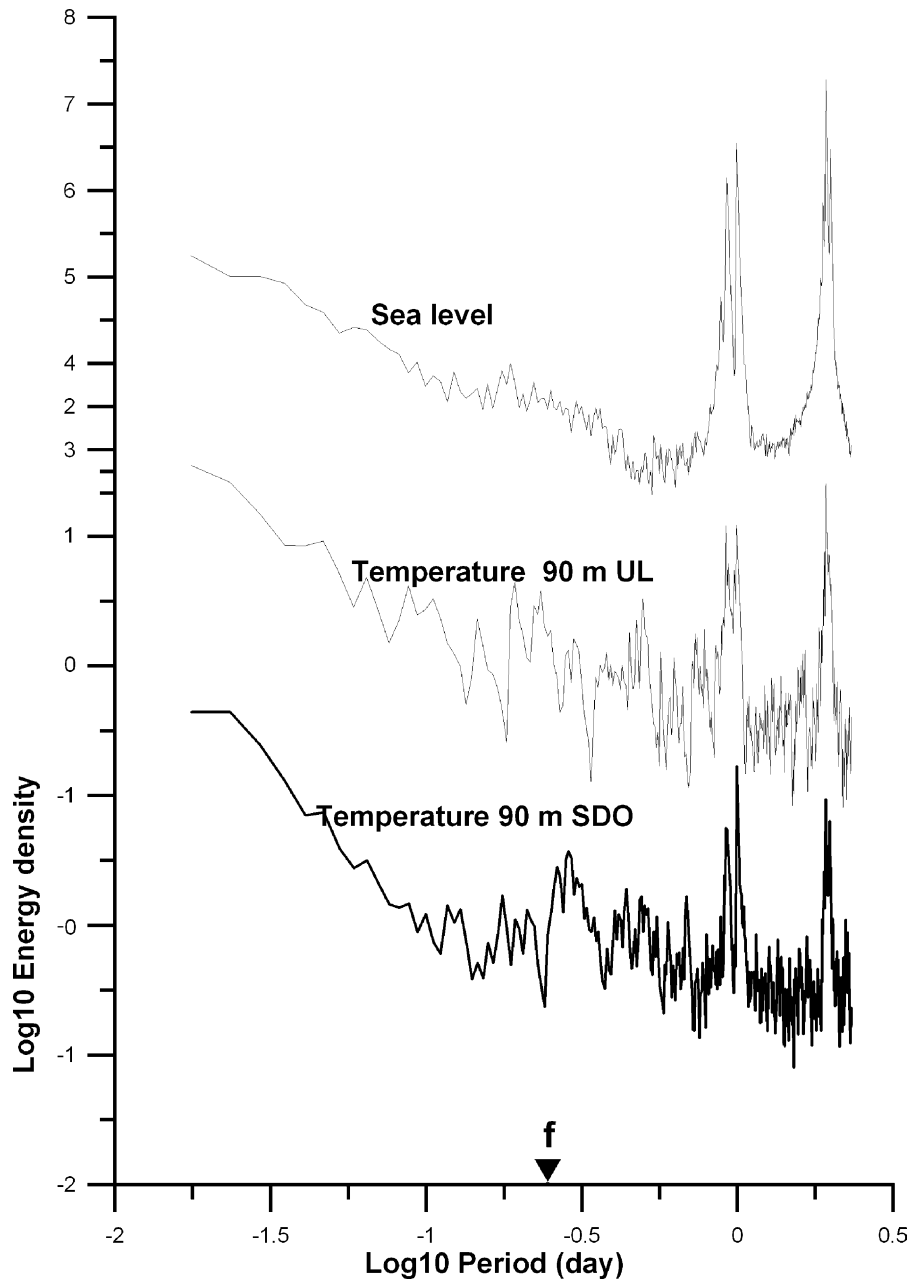


Fig. 5. Energy spectrum of the sea level at Koror, and the water temperature at 90 m depth at the UL and SDO transects. f indicates the inertial frequency.

The sea-level spectrum (Fig. 5) was energetic at diurnal and semi-diurnal tidal frequencies, with the highest peak at semi-diurnal frequency. There was no marked peak at the inertial frequency.

The spectra of temperature at UL and SDO (Fig. 5) showed dominant peaks at diurnal and semi-diurnal frequencies. The highest peak occurred at semi-diurnal frequency at UL and at diurnal frequency at SDO. At both sites there was significant energy at non-tidal, high frequencies, as well as low frequencies. There was no peak at the inertial frequency at SDO, while a peak existed at UL.

The coherence of temperature fluctuations at different depths decreased with increasing depth difference (Fig. 6), while the phase differences were too small to be significant ($<10^\circ$; below 90% confidence level). The coherence was very high at all dominant peaks of the temperature spectra, and was higher at semi-diurnal than diurnal frequencies. There was no coherence at higher frequencies for a depth difference >15 m.

Fig. 7 shows the wavelet analysis for the sea level and for the temperature at 90 m depth at UL. Each panel shows, on top, the time series and, on the bottom, the wavelet transform coefficients for various scales versus

Coherence of temperature signal at SDO

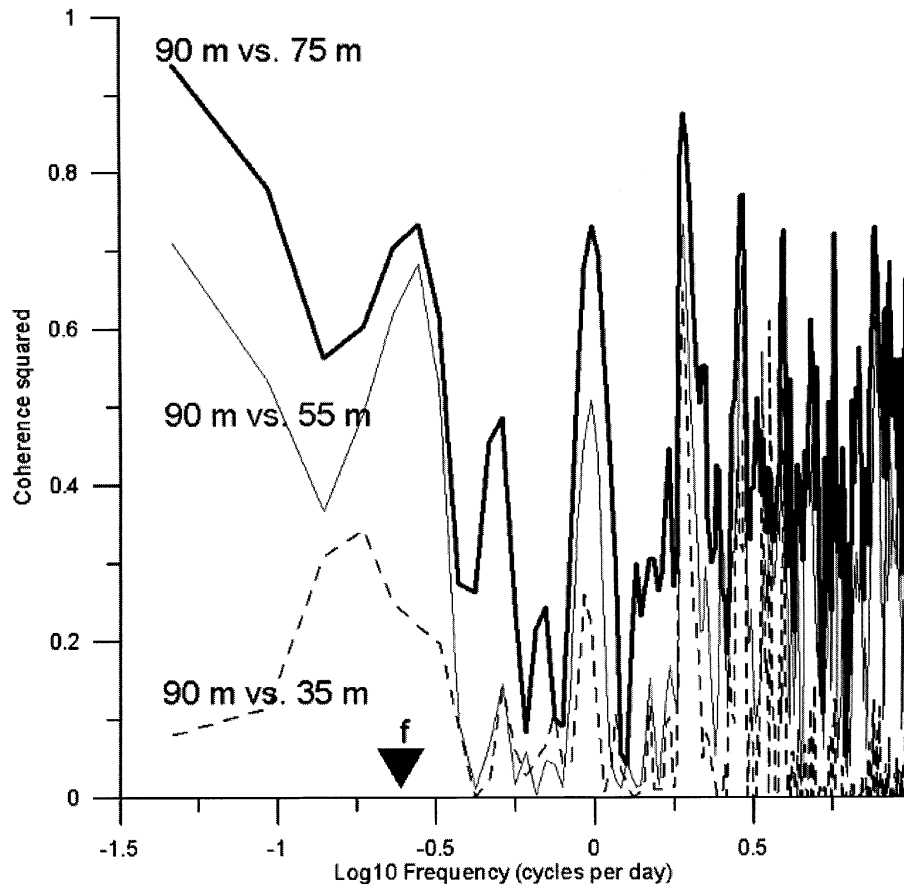


Fig. 6. Coherence squared between water temperature at 90, 75, 55 and 35 m, at the SDO transect. *f* indicates the inertial frequency.

time. The maximum scale used is 16 days. The shading density represents the intensity of the signal in wavelet domain. For the sea level, the wavelet analysis reflects mainly the fluctuations of the tides at semi-diurnal and diurnal frequencies, with the former having more energy. It also shows an event at around 1 July, 2001. This abrupt event is represented by convergence of phase lines from the higher scale toward the time–frequency location where the sudden change occurred.

For the temperature, the wavelet analysis indicates a rather complex tidal signal (Fig. 7b). It also represents the same strong event on 1 July, 2001. This event was found in all the other temperature time series from 90 to 2 m depth for both of the sites (not shown). Other low-frequency events are also apparent; one event occurred around mid-August 2001, and another event, or succession of events, occurred in November–December 2001. The WT of temperature also shows a sharp frequency modulation from 8-day scale to around 3-day scale in November. This might be due to decreasing temperature during that

period, which might have changed the stability and altered the frequency of its normal modes. The time of occurrence of a sudden finite amplitude perturbation and the secular changes giving rise to a frequency modulation signal cannot be easily studied using other spectral techniques such as the Fourier transform.

4. Discussion

Occasional CTD casts near Palau by Saunders and Hastie (1989) and Hata et al. (1998) showed 60 m differences between isotherm elevations from cast to cast, suggesting the presence of internal waves. Our temperature data confirm the presence of these internal waves, and suggest a typical twice-a-day thermocline upwards displacement of 50–100 m, and on one occasion 270 m. This latter wave was probably the largest internal wave yet observed worldwide.

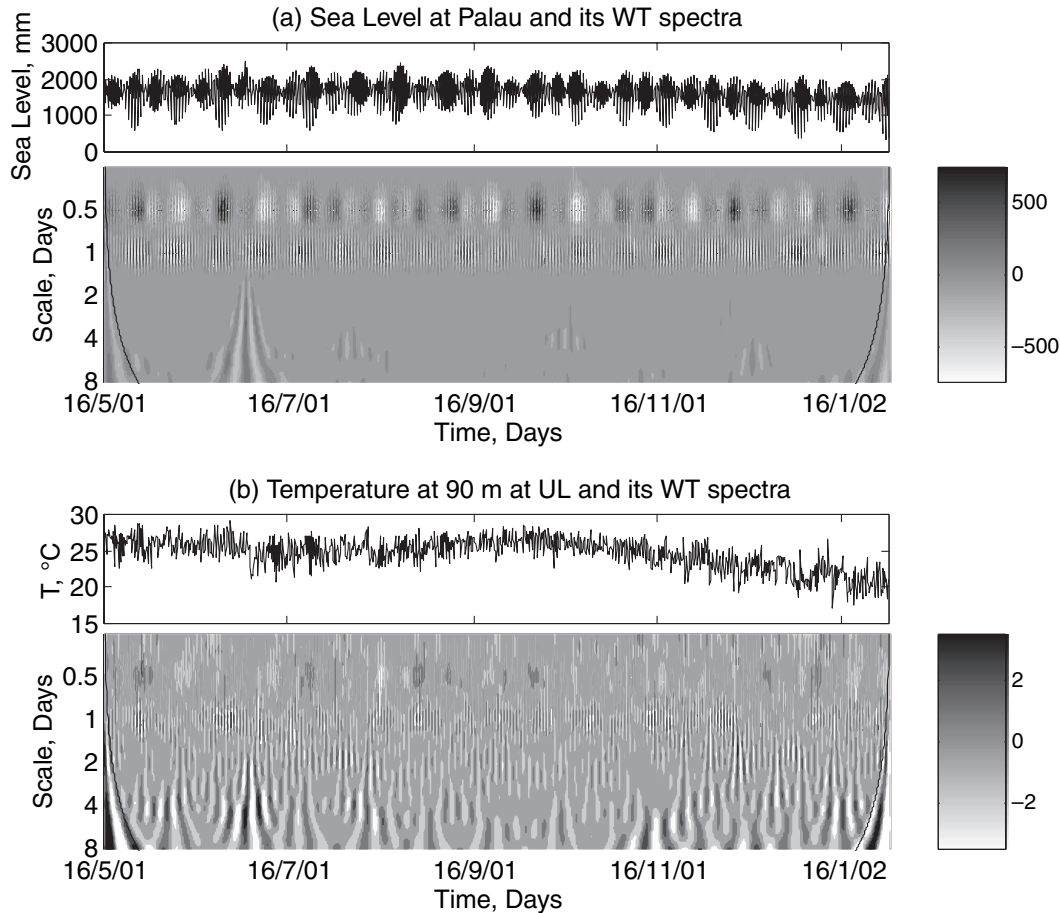


Fig. 7. Time-series and their wavelet analysis using the Morlet wavelet for (a) sea level and (b) the water temperature at the UL transect at 90 m depth, respectively. The wavelet coefficients are calculated for periods <16 days.

The internal wave at Palau occurs at a number of frequencies. There are a number of spectral peaks at diurnal and semi-diurnal frequencies, as well as intermediate and sub-inertial frequencies, less so at the inertial frequency. Large-amplitude internal waves have been detected at higher latitude islands and oceanic islands (Wunsch, 1972; Rancher and Theau, 1988; Wolanski and Delesalle, 1995; Wolanski and Deleersnijder, 1998). At these sites the waves were observed to rotate around the island anticyclonically. Numerical models also suggested that these waves are leaky and therefore that internal waves propagate away from the island, thus contributing to the ocean variability even far away. There were no supporting data for that prediction.

Where horizontal currents impinge on undersea ridges or mountains, internal tides are generated and internal tidal energy flows away from this generation area, as has been documented for the Hawaiian ridge (Ray and Cartwright, 2001; Holloway and Merrifield, 2003). Similarly, oceanic islands also generate internal tides; similarly also, internal tidal energy also flows away from the island, in qualitative accordance with the theoretical predictions of Longuet-Higgins (1969), as was first proposed for the case of Scott Reef, Western

Australia, by Wolanski and Deleersnijder (1998), and is confirmed in this study at Palau.

At Palau the waves generally do not travel around the island because there is no coherence between internal waves on either side of the island. The numerical model (Fig. 8) suggests that the headland at the southern tip of Palau prevents the internal waves to rotate around the island. Internal waves are formed by the tidal and low-frequency currents around the island. Energy is radiated away as internal waves moving away from the island. The model waves are typically 50 m in amplitude.

The model also suggests that at times the internal wave sloshing up the island slope takes the form of a localised tongue of cold water initially moving upwards 180 m along the island slope near the headland (Fig. 8). Such huge amplitude waves have been observed at Palau. The predicted tongue is about 5 km wide and less than 1 km thick. After climbing to maximum height, the intruding cold-water mass falls back downwards by buoyancy and at the same site is advected sideways along the island slope by the tidal currents while losing its tongue-shape by generating high-frequency internal waves. These very-large amplitude internal waves are critical, and laboratory studies suggest that they would

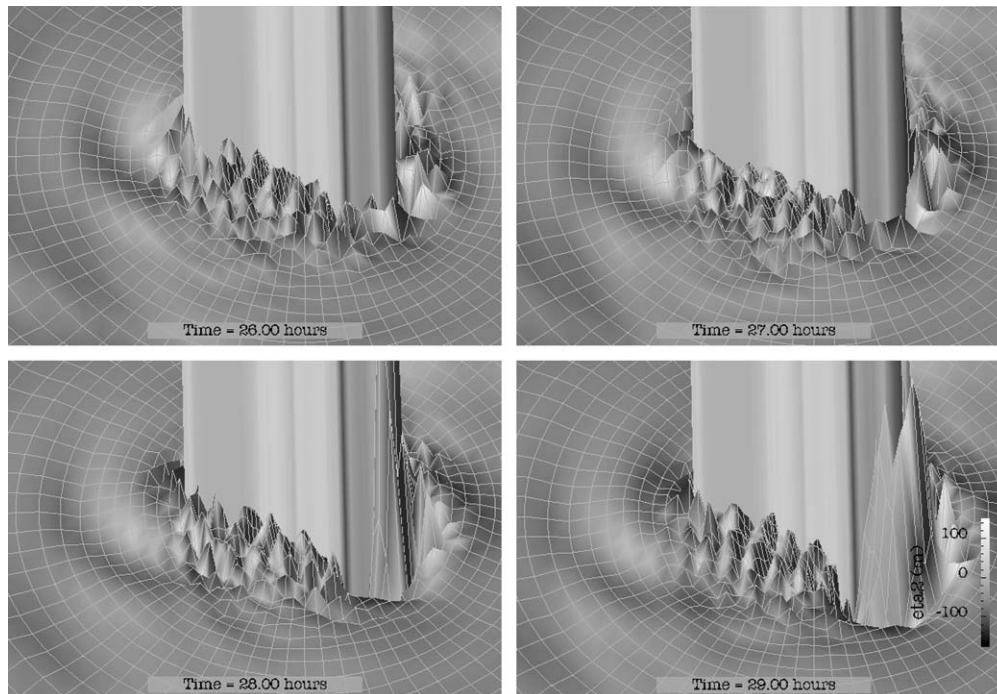


Fig. 8. Three-dimensional rendered examples of the predicted internal wave on the thermocline, resulting from the far-field currents as measured on the FAD site on 6–7 December, 2002. The view is from the southwest and looks towards the southern tip of Palau.

generate a net upward flux of nutrient by mixing (Ivey and Nokes, 1989).

The bulk of the internal waves energy occurred at diurnal and semi-diurnal frequencies. The wavelet analysis revealed that there were, however, events when low frequencies are also energetic. One such event, centred on 1 July, 2001, was associated by the tropical storm Utor that passed near Palau between 1 and 3 July, 2001. However, there are other events of high energy at low-frequencies, such as between November and December 2001, when there were no storms in the vicinity.

The coral reefs at Palau are renowned for lush growth and experienced severe coral bleaching, due to elevated water temperatures, during the worldwide bleaching event of 1998 (Bruno et al., 2001). Although the vertical distribution of temperature was not being monitored at that time, diving observations to the lower limits of coral growth indicate a near eurythermal (30–31 °C) water column to at least 60–90 m depth during summer–autumn 1998. Bleaching occurred to the maximum depths of reef-building corals in Palau. The collection of temperature data reported here was started in response to this event.

The large temperature fluctuations documented have many biological implications depending on the frequency and range of fluctuations. First, they may determine the lower depth limit of coral reef growth. Second, they may limit the number of species and benthic biomass in the zone from the lower limit of coral reefs to depths of 120–150 m.

In most coral reefs, light is believed to be the principal factor controlling the depth limit of reef building. However, this may not be the case in Palau. Water in Palau is generally clear and it seems likely that sufficient light would be present in depths of 50–60 m for coral growth. The absence of coral suggests that temperature stress may be a potential limiting factor controlling the lower distribution of coral reefs in Palau. But it may be the lower extremes of temperature, rather than the upper ranges, which are critical.

Averaged temperature during ‘normal’ years at depths of 90 m in Palau is fully tropical. Mean temperature in 2000 for SDO at 90 m was 25.4 ± 1.9 °C (1 standard deviation), while in 2001 it was 25.38 ± 1.78 °C. Temperatures of 28 °C and higher occurred regularly. The highest temperatures during 1999–2001 at 90 m were 29.3 °C for SDO and 29.28 °C at UL. Thus the mean and upper temperatures seem comfortably within the range for coral growth.

In ‘normal’ years, thermal stress to corals is likely to occur as a result of the temperature minimums, particularly during the internal wave bores documented here, and the range of rapidity of temperature changes. At 90 m depth, temperature in the 17–19 °C range was often recorded. The lowest temperature during this period was 8.45 °C at UL, associated with a deep-water internal wave bore. During that event the temperature decreased by 20 °C. Since these low-temperature events are the result of the internal waves, the waves themselves may limit reef growth at depth.

While thermal stress may determine the lower depth limit of Palauan reefs, the less extreme fluctuations in shallower waters where reefs occur may be beneficial to most reefs. As Fig. 3 indicates, changes of only 1–1.5 °C occur over a few hours' time. Temperature is not a mortality issue, and the rate of change is muted. These rates should pose no physiological problems for corals and other animals. The upwelling of deeper water due to internal waves might in part account for the general 'richness' of Palau's coral reefs through providing a mechanism for nutrient-rich waters to be brought intermittently into oligotrophic surface waters.

Below the depths of coral reef growth, the rapid, short-term temperature changes may well limit what organisms can survive there. The temperature changes at below reef depths documented here are the most extreme found anywhere in world oceans, with the exception of thermal vents. Certainly they are the greatest found in shallow tropical waters, although many other island areas in the open ocean may have similar thermal regimes.

There have been observable changes in the common benthic organisms at 90 m depth at SDO year to year. In May 1997, prior to the 1998 bleaching event, a series of dives were made at 60–90 m depth at SDO to collect benthic organisms. At that time the large benthic ctenophore *Lyrocteis imperatoris*, and the crab *Chirostylus* sp. were extremely common at 90 m. Once the water had warmed at depth (1998 and after), these organisms disappeared at 90 m and above. In 2001 a submersible dive operation at SDO found these two species to not occur above 180 m. In May 1997 some dying sponges were seen at 90 m, an unusual occurrence based on past experience, indicating possible low-temperature stress. Those organisms that can move vertically, such as *L. imperatoris* and *Chirostylus*, may stay within a particular temperature range and change depth to compensate. Rapid temperature changes, however, may pose an additional problem and be an absolute limit to occurrence in that zone. For species that cannot move, such as the sponges cited above, they may simply be excluded from areas, resulting in the potentially depauperate nature of the slope beneath reefs where there are internal wave-mediated temperature extremes.

Another indication of the relative paucity of organisms on the deep reef of Palau comes from Pyle (2001) video transects at 90 m depth at SDO. Pyle found 37 individual fishes representing 24 species. A similar video recording transect made in Papua New Guinea at 110 m depth had more species and 10 times the number of fishes in the same time period as were found on the Palau transect.

It would be useful to assess the species richness and biomass in other areas of the tropical west Pacific with more stable temperature regimes as compared to the thermally dynamic environment in Palau.

In the Great Barrier Reef the interaction of bathymetry, oceanography and biological processes help determine biodiversity (Wolanski, 2001). The bathymetry of Palau is even more complex and rugged with headlands, canyons and deep embayments. Because the internal waves are enhanced by a complex bathymetry, the high biodiversity of Palau coral reefs, as well as their temporal and spatial variability, may thus similarly result from the complex bathymetry.

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