Mesophotic Coral Ecosystems

A lifeboat for coral reefs?

3.6. **Spotlight on the Palau Island group**

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Having been the focus of research for over 20 years, the MCEs of Palau are among the best-documented MCEs. Little research has been conducted in other areas of the tropical Indo-West Pacific, although a vast number of MCEs occur there. The great majority of research has been done around the main Palau Island group. The northern atolls, southwestern oceanic islands and low latitude Helen Reef atoll are not included in this case study. The MCEs of Palau have been investigated using standard and mixed-gas diving and small submersibles (Colin 1999, 2009). Mesophotic invertebrates were identified through collections for the U.S National Cancer Institute natural product screening programme (1994–2014), and fish are also well known (e.g. Myers 1999). Temperature monitoring arrays to 90 m depth were established after the 1998 bleaching event. Aspects of Palau's MCEs are included in Colin (2009) and additional information is included here.

The outer margins of Palau, including the outer islands and atolls, generally have MCEs continuing below shallow reefs. The main island group reef system has approximately 300 km of barrier and fringing reef, with 80 per cent or more of this having a mesophotic component. This roughly 260 km long MCE covers approximately 24 km^2 (increasing to approximately 30 km^2 if Angaur, Kayangel and Velasco Reef are included). MCEs also occur in the deep channels in the barrier reef (to 80–90 m), as deep patch reefs within the lagoon (up to 55 m) and shallower lagoon area (30–36 m) with low light and high sediment.

Reefs built on the basaltic Palau-Kyushu Ridge have grown in shallow water since the Miocene, laying down extensive layers of carbonate rock. Some have been uplifted to form the Rock Islands, while other areas (i.e., Kayangel Atoll, Velasco Reef and the northern reef tract of the main Palau group) have subsided, with up to 1,000 m of carbonates deposited on top of the basaltic basement. The present MCEs developed only in the last 20,000 years as sea level rose from the last glacial lowstand of –120 m.

In general, the mesophotic zone of the outer slope of Palau's reef ranges from steep (20–30° slope) to vertical, and is usually a narrow strip, often less than 100 m wide. On shallow reefs (10–40 m range) there is a distinct relationship between outer reef slope angle and exposure to winds and waves (Figure 1). Vertical to near-vertical slopes are found largely where the reef faces to the southwest or south, whereas those reefs exposed to the west, through to the north or the east, are gentler, with slopes usually in the 20–45° range. Deeper slope MCE geomorphology does not necessarily mirror the shallower reefs. Many areas with near-vertical shallow slopes have the MCEs sloping in the 30–45° range, with a distinct slope at some point. In other areas vertical MCE faces occur, with or without vertical shallow reefs (Figure 2).

The downward movement of sediment and reef rock controls the structural aspects of most MCEs. Build-ups of talus and sediment produce occasional downslope movements of materials and serve to limit areas suitable for stony corals (cf. Figures 3a and 3b). Vertical faces have areas protected from downwelling materials by overhanging ledges. Erosional channels located at intervals along these faces act as sediment chutes to convey reef debris to the depths.

A number of Palau's MCE faunal elements are now relatively well known, with Colin (2009) covering overall levels of species diversity, including many mesophotic groups.

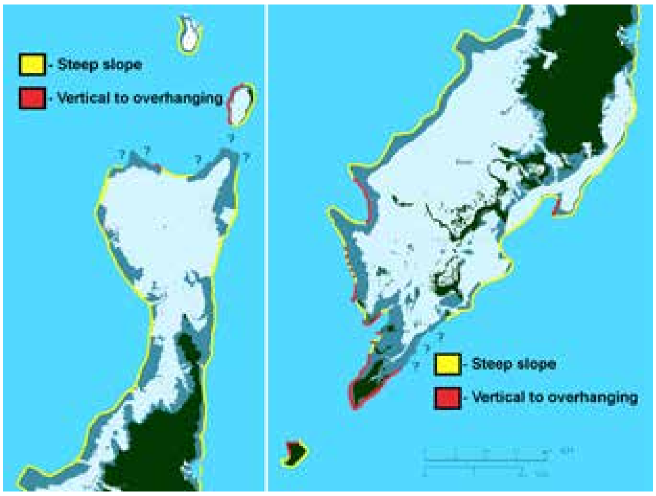

Figure 1. The slope of the outer reef face of Palau to depths of 50 m is related to wind and wave direction. Deeper MCE slopes do not show a similar correlation (from Colin 2009).

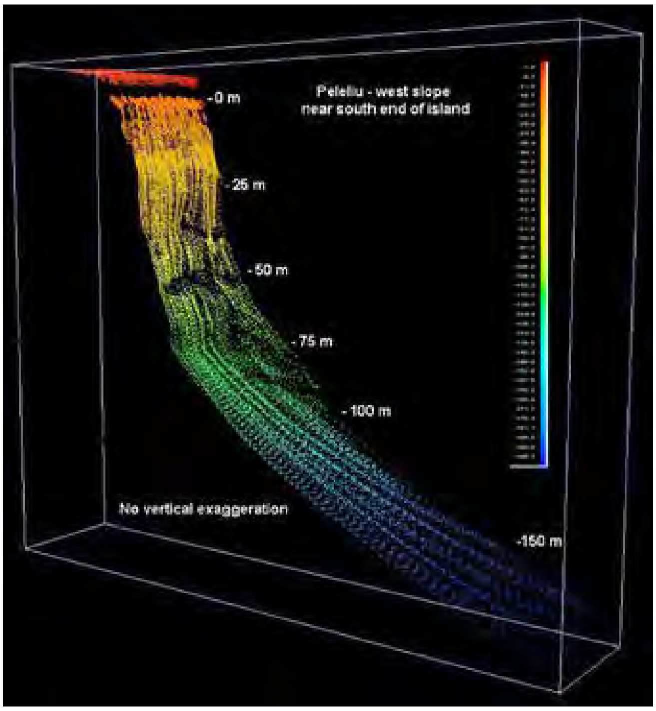

Figure 2. An example of an outer reef slope from southwestern Peleliu, Palau, imaged with multibeam sonar. This area has a very steep escarpment with near-vertical faces to depths of 70–90 m, and then slopes more gently to oceanic depths.

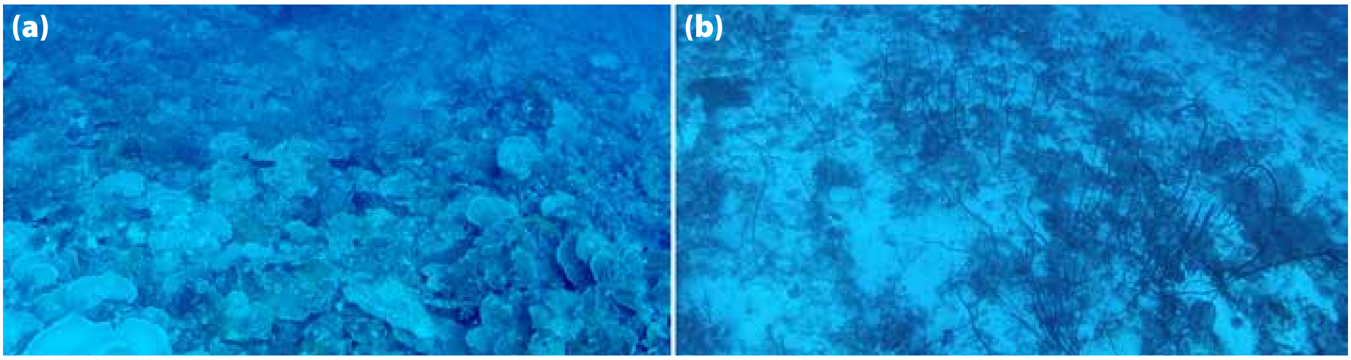

Figure 3. Deep slope MCEs at two locations in Palau. (a) Sloping bottom with very high coral cover (estimated 75 per cent) at 50 m depth on the western side of Ngeruangel reef, Palau. (b) Sloping bottom on a western-facing MCE, with low stony coral cover, many whip gorgonians and downslope sediment transport (photos Patrick L. Colin).

Scleractinian corals

While Palau's stony coral diversity is relatively high (roughly 320 species), it is limited in Palau's mesophotic zone (Veron 2000). The lower depth limit for the genus *Acropora* is about 45 m. The only branching coral commonly found at depths below 60 m is *Madracis asanoi*, growing as relatively short twisted branches in colonies up to one metre across. It is also found encrusting dead black corals or gorgonians. The coral is zooxanthellate, apparently the deepest such coral in Palau, down to about 90 m (Figure 4a), then continues deeper, becoming azooxanthellate (Figure 4b).

Most other mesophotic stony corals are plate-like with thin skeletons, typified by the genus *Leptoseris*, and are horizontally oriented to capture light (and are vulnerable to accumulating sediment). At least 22 species of ahermatypic and azooxanthellate, largely solitary, stony corals are also found in the mesophotic, some of which are illustrated in Veron (2000).

Other Cnidaria

The gorgonians and soft corals of Palau are relatively well known, with about 52 species (Alderslade 2002, Williams 2003, Fabricius et al. 2007, Colin unpublished); a number of which remain undescribed. Large seafans of *Anella* and *Muricella* and a number of whip gorgonians (Figures 3b and 5a) are common along the slope. The delicate yellow gorgonian *Stephanogorgia faulkneri*, described from Palau, is spotty in its distribution, but indicative of mesophotic conditions where it occurs (Figure 5d). Other MCE cnidarians include stylasteridae, about a dozen black corals (Opresko 2004), and an assortment of anemones (Arellano and Fautin 2001, Fautin and den Hartog 2003) and hydroids.

Other invertebrates

The known MCE sponges (Porifera; Figures 5b and 5c) currently number at least 30–40 species. A number are "lithistid" or stony sponges, some of which build reef structure at mesophotic depths — an ability comparable to Western Atlantic sclerosponges. Other noteworthy MCE invertebrates include the large benthic ctenophore *Lyrocteis imperatoris,* which perches atop gorgonians and black corals and extends its tentacles to feed (Figure 5e). It is motile to an extent and has been documented to change its depth range with changing water column structure related to El Niño Southern Oscillation events.

Among molluscs, the large oyster *Empressostrea kostini* occurs beneath ledges at 60–90 m, where it is protected from downwelling sediment (Figure 5f). The Palau chambered nautilus, *Nautilus belauensis* (Figure 5g), is a mesophotic species, which has seen a number of studies on its occurrence and environment (Carlson et al. 1984, Saunders 1984, Ward et al. 1984, Hayasaka et al. 1995, Kakinuma 1995, Okytani

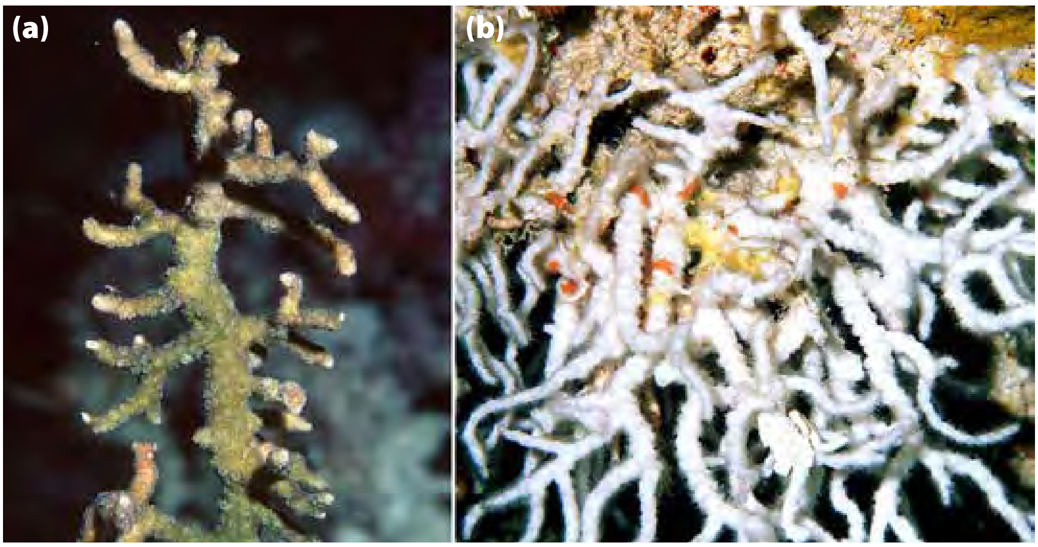

Figure 4. (a) The deep-dwelling branching stony coral *Madracis asanoi* is zooxanthellate at depths of 60–90 m. (b) It becomes azooxanthellate on vertical faces at 120 m depth (photos Patrick L. Colin).

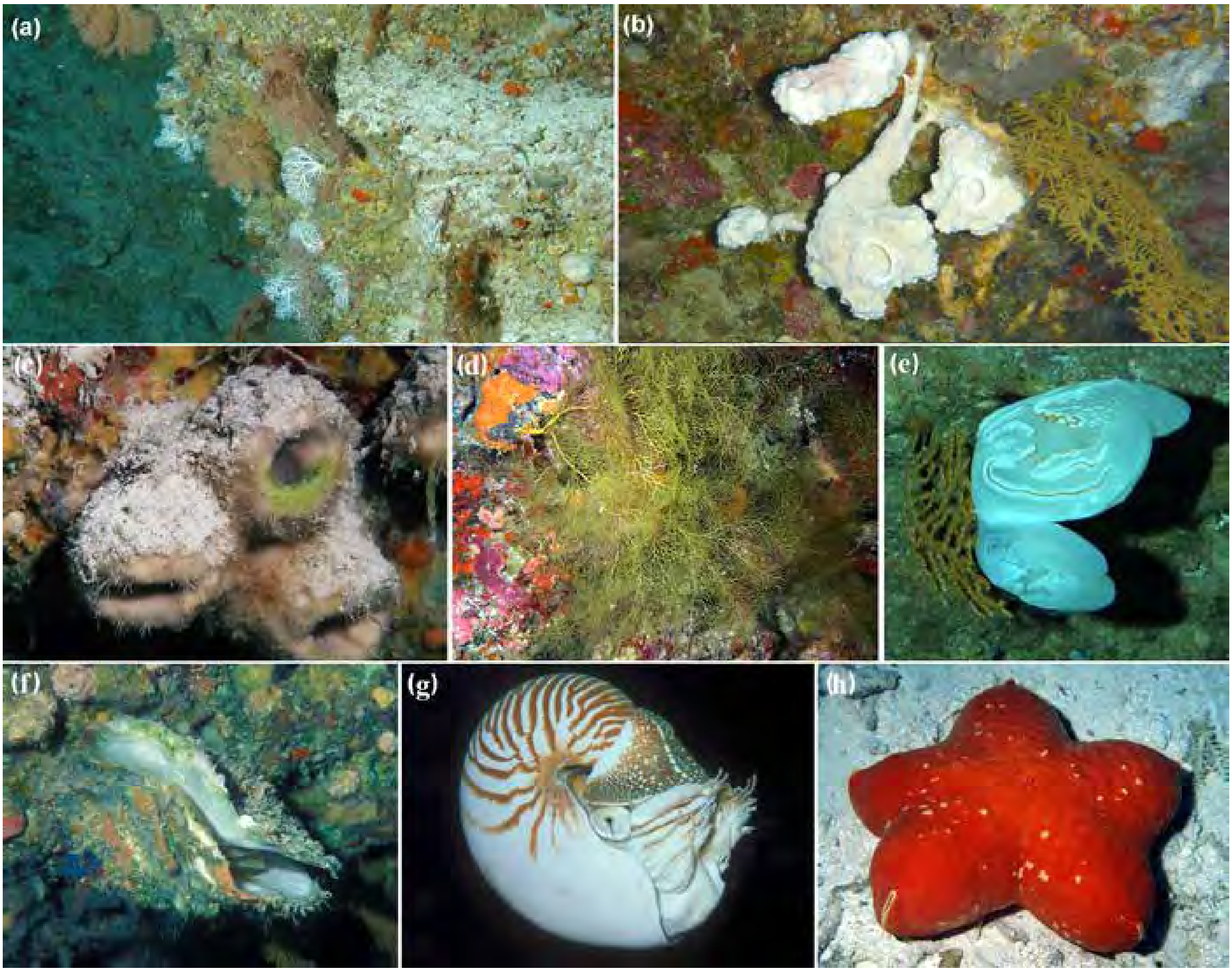

Figure 3. (a) Overhanging reef face, 80 m depth dominated by gorgonians and stylasterine corals. (b) The mesophotic sponge *Aplysinella strongylata* is found scattered on near-vertical reef faces. (c) The lithistid sponge, *Scleritoderma hermanni*, is common below 80–90 m depth. (d) The delicate gorgonian *Stephanogorgia faulkneri* is common along some MCE slopes. (e) The benthic ctenophore *Lyrocteis imperatoris* is a motile species occurring as shallow as 90 m during El Niño conditions. (f) The large oyster, *Empressostrea kostini*, occurs in small caverns at 60–90 m depth sheltered from sediment downflow. (g) The Palau chambered nautilus, *Nautilus belauensis*, is found at the lower limit of the mesophotic zone. (h) The sea star *Astrosarkus idipii* is found on steep slopes at 70–120 m depth (photos Patrick L. Colin).

and Kurata 1995). Similar species occur throughout the Indo-West Pacific, with temperature largely controlling their depth distribution.

Mesophotic echinoderms include the large sea star *Astrosarkus idipii* (Figure 5h; Mah 2003) and a considerable variety of other species (Mah 2005). The few ascidians (Chordata) known from the mesophotic zone in Palau include species not known from other environments.

Fish

Known reef fishes of Palau were described by Myers (1999), but there are still new species and geographic records being

Figure 6. Recently described mesophotic reef fish from Palau. (a) *Chromis abyssus*, (b) *Centropyge abei*, (c) *Hippocampus denise* on the gorgonian *Muricella* spp., and (d) *Glossogobius colini* (photos Patrick L. Colin).

discovered, including in the mesophotic zone (Figure 6). One example is the pygmy angelfish, *Centropyge abei* (Allen et al. 2006)–unknown until direct investigation of the mesophotic was undertaken (Figure 6b). The small seahorse, *Hippocampus denise* (Figure 6c) is known elsewhere from shallow reef habitats, but in Palau is only found in the 35–80 m depth range, where its host gorgonians, *Muricella* spp., occur.

Macroalgae

Little is known about the mesophotic macroalgae from Palau. Green algae that do occur within the mesophotic, are members of the genus *Halimeda* and at least one other flattened species, presently unidentified (Colin 2009). Coralline algae occur at mesophotic depths, but are poorly known. There are no seagrasses below approximately 35 m in depth.

Pharmaceutical discoveries

Palau has been an important site for the collection of samples for drug development research, with well over 100 publications (as of 2004) on its natural marine products (Faulkner et al. 2004). Some chemically interesting samples have come from mesophotic depths (Qureshi et al. 2000, Sandler et al. 2006).

Physical Characteristics

Sloping areas in the mesophotic zone often have alternating cascades of rubble and sediment. Low percentages of stony corals often grow on the stable rubble, but deep slope environments are dominated by gorgonian fans, with some genera limited to deeper depths (Fabricius et al. 2007). The water close to the outer reef faces of Palau is not particularly clear compared with oceanic “warm pool” water, and may limit depths to which low-light scleractinian corals can grow. However, water temperatures may prove to be more significant in limiting the lowest depth of zooxanthellate coral growth.

The horizontal distance between the mesophotic and the shallow reefs is small, usually less than 100 m, but density stratification can restrict water exchange between shallow and deep regions. Stratified oceanic water moving inshore through channels on rising tides can be thoroughly mixed by turbulence, while the water exiting on falling tides remains mixed (Colin 2009).

Palau is in an area of very active internal waves (Wolanski et al. 2004); probably not unusual for tropical Western Pacific reef environments, but underappreciated as a mechanism influencing the ecology of MCEs. Over 15 years, weekly mean shallow reef water temperatures (10–15 m depth) ranged from 27.5° to 30° C, with only a 1–1.5° C annual range (Figure 7). In contrast, MCEs had a greater range, with two types of temporal dynamics. First, medium-term week to month variations in mean temperatures (weekly means at 57 m ranged from 21°–29.5° C) are related to the El Niño Southern Oscillation or other undetermined conditions and are essentially uncoupled from temperatures on shallow reefs. Second, internal waves produce rapid short-term changes (several degrees Celsius in an hour or less; Figure 8), upwelling cool, nutrient-rich waters at times to the benefit of shallow reefs. Combined with medium-term variation, this produces a thermally challenging environment, which is probably a major factor limiting the lower depth of MCEs in Palau.

During La Niña periods, such as in August 2010, the temperature stratification on MCEs ceases to exist, with mesophotic temperatures equalling those of shallow reefs and coral bleaching occurring at all depths (Bruno et al. 2001, Colin 2009). The oceanic water column around Palau can change very rapidly between El Niño and La Niña periods. For instance, the temperature, salinity and chlorophyll fluorescence determined by Spray gliders near the barrier reef in 2010 during El Niño (February) and La Niña (August) periods, only 200 days apart, exhibited tremendous differences (Figure 9). A similar shift almost certainly occurred during the 1997–1998 coral bleaching event. MCEs will have to accommodate these rapid shifts if they are to survive.

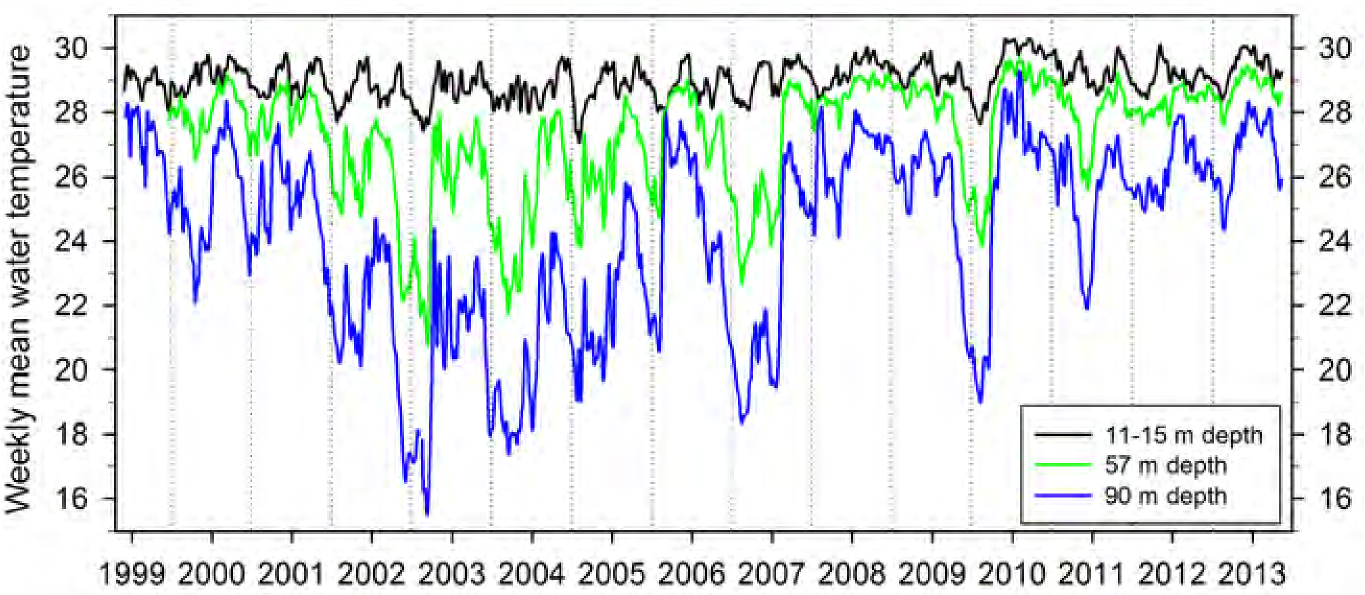

Figure 7. Weekly mean water temperature on the outer slope over 15 years has shown much greater variation in the mesophotic zone (57 and 90 m) than in shallow water (11–15 m).

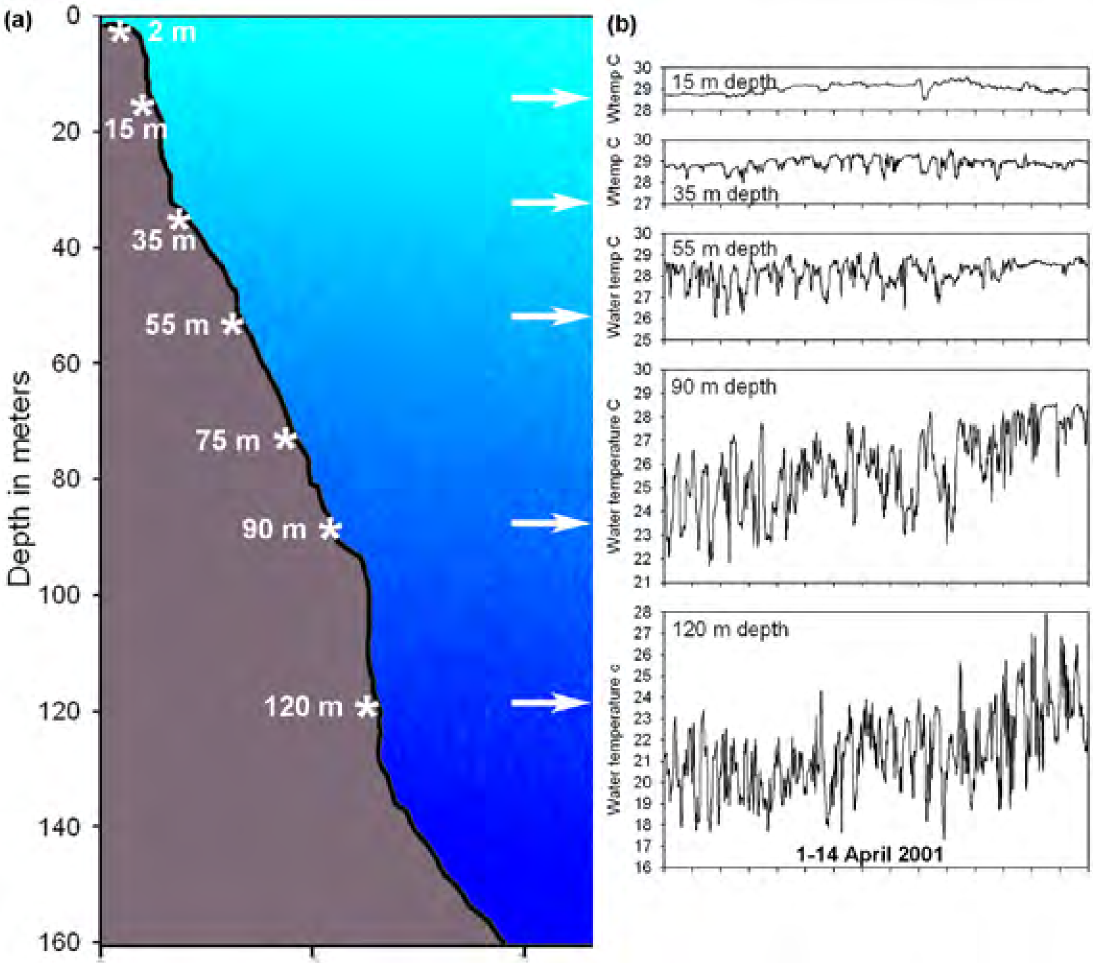

Figure 8. The mesophotic zone in Palau has a large variation in water temperature over short time periods (hours to days) due to internal waves impacting the outer slope. At depths of 50–90 m, the water temperature essentially becomes uncoupled with that of shallow reefs. Internal waves also upwell cool nutrient-rich waters at times (from Colin 2009).

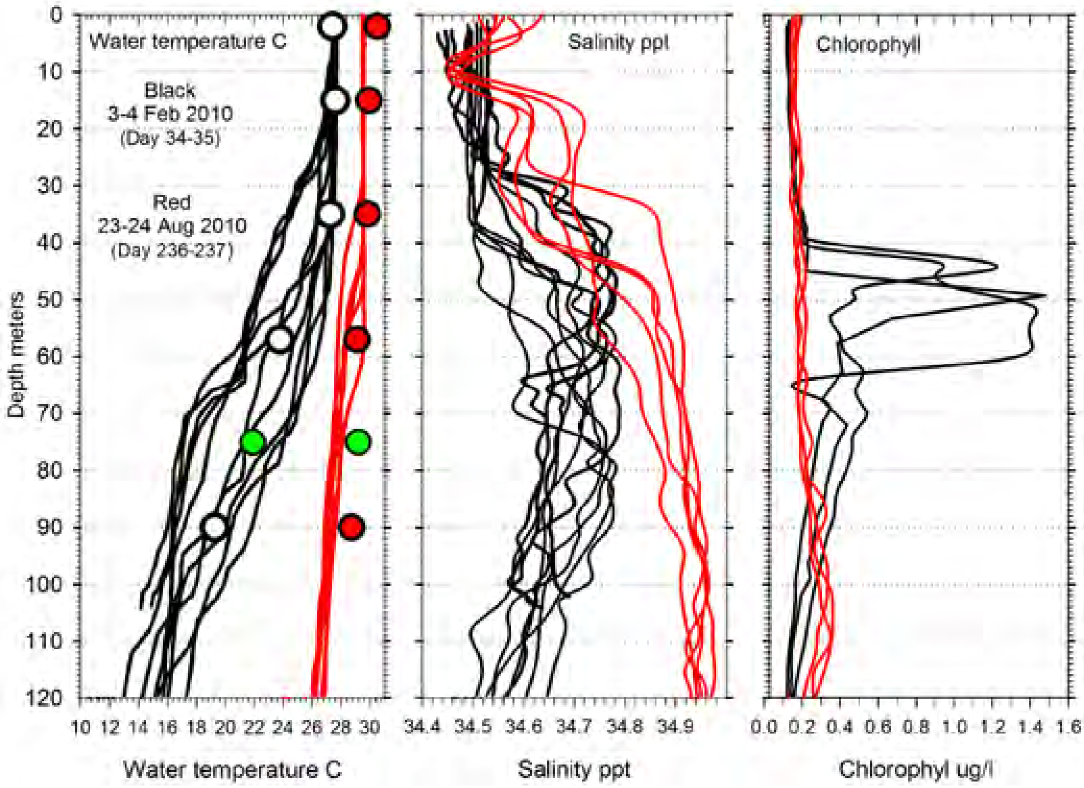

Figure 9. Water column conditions adjacent to the western barrier reef in 2010 determined by Spray gliders during El Niño (February) and La Niña (August) periods (only 200 days apart) were quite different, with a chlorophyll maximum as shallow as 40–50 m during August. (Data courtesy of Dan Rudnick, Scripps Institution of Oceanography).

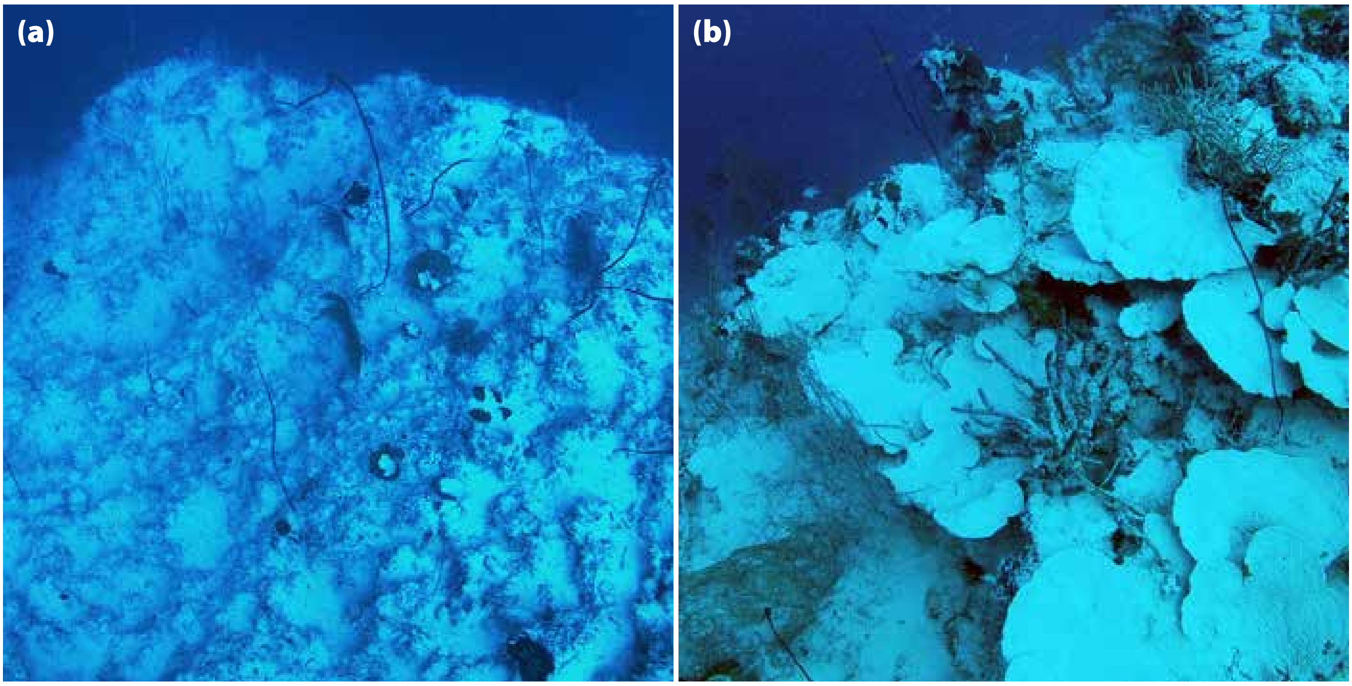

Figure 10. Typhoons can cause coral mortality at mesophotic depths through deposition of sediment suspended by wave action and reef destruction. (a) View downwards from 50 m to 80 m, Short Drop Off, Palau, two months (January 2013) after Typhoon Bopha. (b) Flattened stony corals adapted for light capture at 45 m in depth were smothered by several millimetres of fine sediment suspended by Typhoon Bopha (photos Patrick L. Colin).

It is assumed that there is upwelling of cooler, nutrient-enriched water into the shallow reef environment during El Niño periods, but such dynamics are not documented. Shifts in the "nutricline" over nearly a century (based on cross-sections of large gorgonians from 80 m) have been examined by Williams and Grottoli (2010).

Typhoons and tropical storms

Typhoon and tropical storms have affected Palau's MCEs in several ways. With steep or vertical slopes, extreme storm events can generate reef rubble and sediment in shallow water, which moves downslope, causing damage to all benthic communities. Typhoon Bopha in December 2012 caused massive destruction of shallow and mesophotic reefs on the eastern side of Palau. Wave action broke loose reef materials, causing massive debris slides down the slope and producing rubble berms on shallow reefs. In the weeks following the typhoon, suspended sediment was transported to distant areas that had not been impacted directly by waves, where it settled, blanketing reefs and smothering mesophotic corals (Figure 10).

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In memory of Dr. John J. Rooney (1960–2016) and his dedication to exploring and understanding mesophotic coral ecosystems.

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Cover photo: Bright blue ascidians, known as sea squirts, are found thriving at 50 metres (164 feet) among corals, greenish brown algae (*Lobophora*) and red, orange, and brown sponges off La Parguera, Puerto Rico (photo Héctor Ruiz).

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