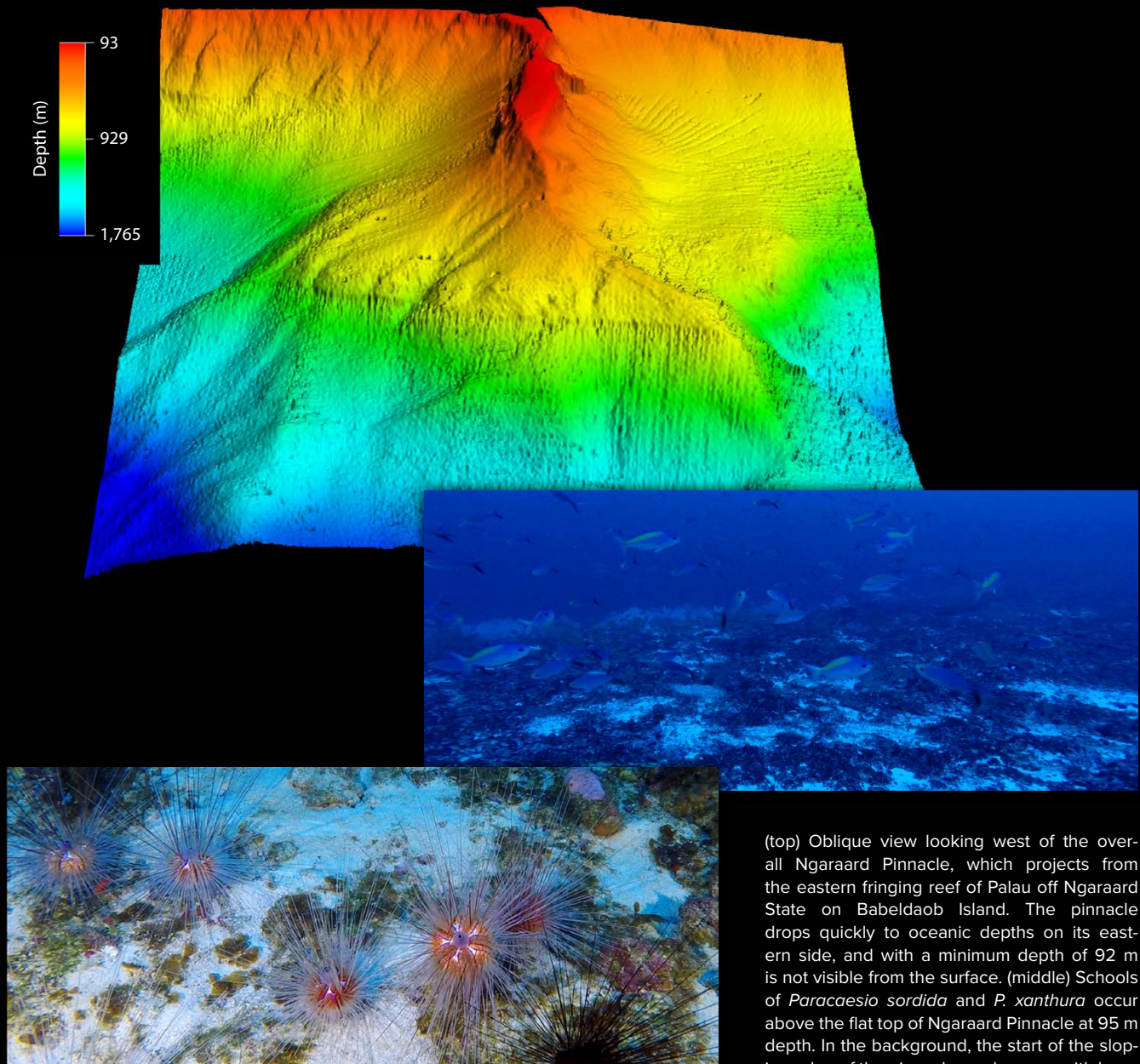


NGARAARD PINNACLE, PALAU

AN UNDERSEA “ISLAND” IN THE FLOW

By Patrick L. Colin, T.M. Shaun Johnston, Jennifer A. MacKinnon, Celia Y. Ou, Daniel L. Rudnick,
Eric J. Terrill, Steven J. Lindfield, and Heidi Batchelor



(top) Oblique view looking west of the overall Ngaraard Pinnacle, which projects from the eastern fringing reef of Palau off Ngaraard State on Babeldaob Island. The pinnacle drops quickly to oceanic depths on its eastern side, and with a minimum depth of 92 m is not visible from the surface. (middle) Schools of *Paracaesio sordida* and *P. xanthura* occur above the flat top of Ngaraard Pinnacle at 95 m depth. In the background, the start of the sloping edge of the pinnacle can be seen with large numbers of pale primnoid gorgonians present. (bottom) Sea urchins such as these are the only herbivores known from Ngaraard Pinnacle. They evidently feed on the thin algae cover at 95–100 m depth, some of the deepest herbivory known in the ocean.

ABSTRACT. This paper uses the Flow Encountering Abrupt Topography (FLEAT) experiment's unique data set to examine and document the biophysical environment of an unusual low-light reef habitat in the western tropical Pacific Ocean. Located 1.6 km seaward of the eastern coast of Palau, Ngaraard Pinnacle (NP) rises from the deep ocean to 92 m depth, constituting an “island” where such a habitat exists. Low-light reef habitats have not been well studied and are different from those of typical shallow reef systems. Water temperatures recorded at NP using bottom-mounted temperature loggers vary on two timescales, from hours to days and over months, related to the El Niño-Southern Oscillation (ENSO). This environment is subject to tremendous temperature variability; from 2010 to 2019 temperatures were below or near the lower limits of life for photophilic reefs for months. Mean temperatures shifted 10°–12°C in six months, with low values associated with El Niño and high values with La Niña. The ENSO-related temperatures at NP were similar to those recorded at stations along the main reef, making it among the most variable environments observed in the tropical western Pacific. The stratified water column above NP was subject to sheared currents moving in opposite directions. In this variable physical environment, the biological community is characterized by a modest number of reef invertebrates, very low algal cover, and a diverse and abundant reef fish community. The biophysical data collected at NP show how this rarely observed environment supports the observed community.

INTRODUCTION

In the tropical western Pacific, many island/reef areas rise steeply from the deep ocean to depths at or near the surface and are major impediments to otherwise unrestrained upper ocean flow. Where ocean currents do encounter islands and their reef communities, they are deflected. Flows will move along the steep slopes of shallow barrier and fringing reefs, while at topographic features, such as headlands, flows may separate, generating eddies that affect both retention and dispersal of planktonic larvae from benthic marine communities (Hamner and Largier, 2012).

Baldwin et al. (2018) describe three reef faunal zones based loosely on depth and light penetration: altiphotic (high light, surface to 30–40 m depth), mesophotic (intermediate light, 30–150 m depth), and, coining a new term, “rariphotic” (low light, 150–300 m depth in clear tropical waters), and the aphotic zone, with no surface light, lies beneath 300 m. The mesophotic has also been divided into poorly defined upper (30–40 to 70 m depth) and lower (70–150 m) zones whose depth limits differ by location (Baker et al., 2016). In addition to light, the zones may be distinguished based on temperature (Colin, 2018) and faunal composition (Baldwin

et al., 2018; Stefanoudis et al., 2019).

The relationship between shallow currents (surface to ~30 m), waves, and reef communities has been extensively investigated (Monismith, 2007; Lowe and Falter, 2015), but oceanographic conditions at the base of the mixed layer (~100 m depth) near reefs are less known. Temperatures are usually cooler and more variable (Colin, 2018), and deep environments may be subject to currents that flow opposite to surface currents. If the sheared flows are unstable and produce turbulent mixing, these strong flows impact biological communities. In the relatively rare situation where a small area of hard bottom occurs surrounded by much deeper water, the isolation from shallow communities and near-surface conditions results in unusual “deep reef islands.”

The data collected by the Flow Encountering Abrupt Topography (FLEAT) experiment in the western tropical Pacific show how the physical characteristics and biological communities of deep reef islands differ (or not) from other reefs of similar depths. FLEAT provided coincident observations of physical conditions and community composition at the elevated deepwater structure called Ngaraard Pinnacle (NP). NP is located 1.6 km east of the eastern fringing reef

in Ngaraard State on Babeldaob, Palau's largest island (Figure 1a–d). With a shallowest depth of 92 m, the flat-topped rise measures about 400 m east to west and 150 m north to south (the area above the 100 m isobath is approximately 0.04 km²). NP constitutes an ideal “island” of hard bottom habitat separated from other reef bottoms by deeper water and divorced from many elements that allow shallow reefs to thrive. In addition, the upper surfaces of NP are near the lower limits of light and temperature for the growth of photophilic coral reefs.

Because of the steep profiles along the 300 km long margin of Babeldaob's outer reef (Figure 1a), the mesophotic (Colin and Lindfield, 2019) and rariphotic zones are often only found in narrow bands paralleling the shallow reef. The transport of shallow-water sediment/rubble, detritus, and particulate organics to depth by diverse mechanisms, from normal wave action to violent cyclonic storms, is evidenced by chutes and reentrants on reef faces (Colin and Lindfield, 2019). Accumulations of talus and sediment occur where ledges exist and in areas and at depths where slopes decrease. Because NP lacks upslope benthic environments, it provides a unique environment for contrasting the similarities/differences between general reef/island slopes and this isolated/sheltered area.

While the presence of this deep-water “bank” has been known to fishermen for some time (Chapman, 1988), the general area of the pinnacle was not surveyed with multibeam sonar until the FLEAT research cruise aboard R/V *Roger Revelle* in July 2013. The survey was completed in early 2019 when the Coral Reef Research Foundation's catamaran *Kemedukl* mapped the shallowest area of the pinnacle. Figure 1b–d merges the data sets from the *Revelle* and *Kemedukl* cruises. The biological communities occurring on NP were at that time unknown, and the site offered a fresh opportunity to examine whether such deep structures might constitute “refugia” (Bongaerts and Smith, 2019) from con-

ditions associated with the decline of shallow reefs (answer—they do not). In other regions, such as Hawai'i, stony corals form such communities at depths of 110–120 m (Spalding et al., 2019), but no comparable deep coral communities are known from the outer reef slope areas of Palau (Colin and Lindfield, 2019).

The data collected at NP characterize the geological and physical environment, as well as the faunal distribution, establishing how this rare habitat—the first described in the Pacific—is able to support life.

METHODS

Qualitative assessments of benthic communities and fish abundance were determined from deep camera video and photo transects and five scuba dives on the flat top of NP. Two types of camera systems were used. The first had downward-pointing still and video cameras without lighting that were maintained 6–15 m above the bottom by a line with a surface float that incorporated position-logging GPS. The system drifted with the current, and the resultant images/video were used to prepare geolocated mosaics of the

bottom. The second system had a frame with two video cameras and lights lowered by line to rest on the bottom and record oblique video while a surface GPS logged positions. It was moved across the bottom by lifting the frame with the line, letting it drift for a short period, then setting it down again. The detailed color video recorded allowed us to identify species and determine bottom characteristics. Diving observations at NP were made using mixed-gas diving for deployment/recovery of temperature loggers and limited collections of organisms.

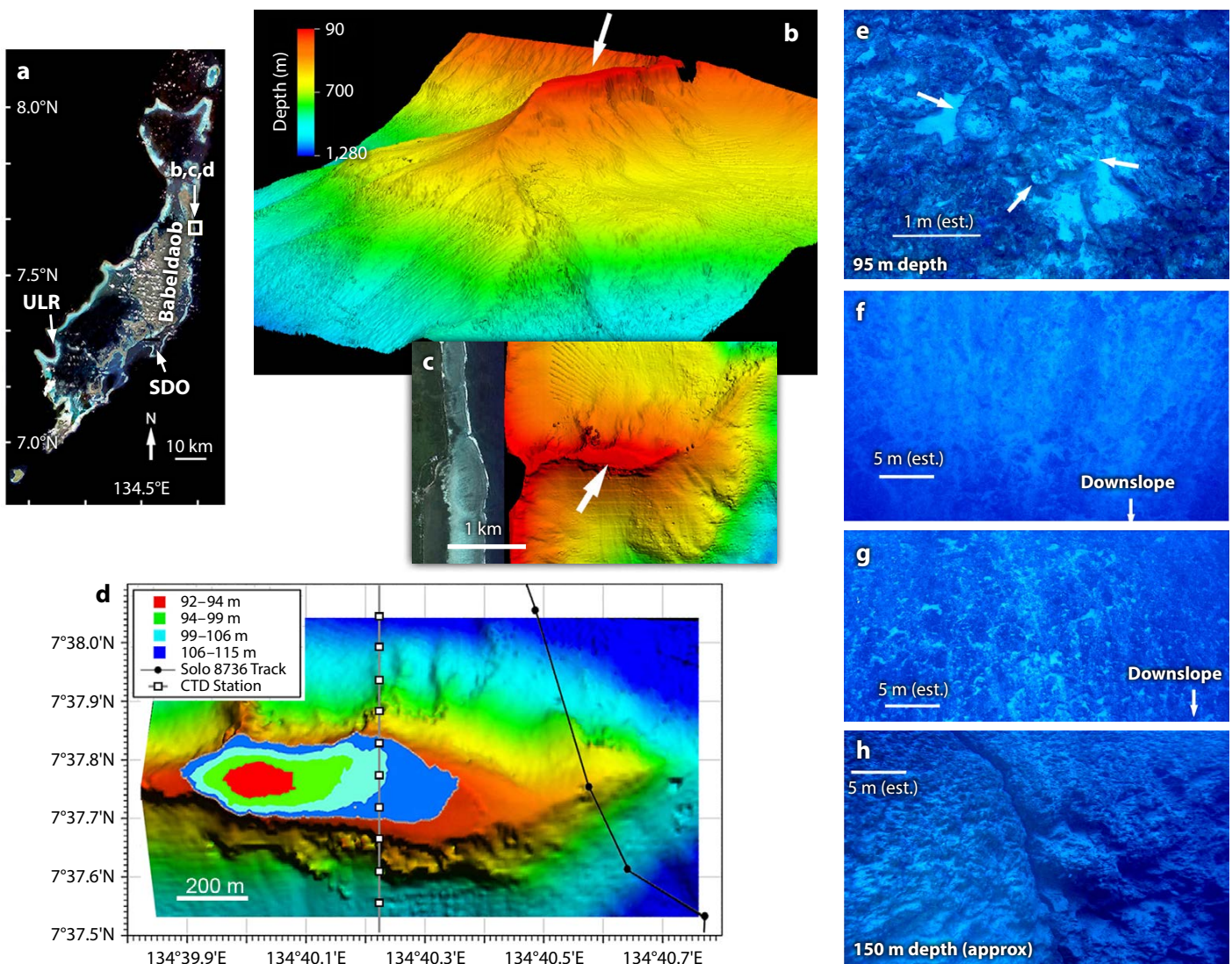


FIGURE 1. (a) Study areas are located on a satellite image of the main Palau reef/island tract. Ngaruaard Pinnacle (NP) is located within the white box, and Short Dropoff (SDO) and Ulong Rock (ULR) are indicated. (b) NP (white arrow) is shown in oblique view to indicate topography, and (c) provides a vertical view of NP (white arrow) showing its relationship to the fringing reef. (d) Bathymetric map of NP showing breakdown of depths on the flattened top. The black line tracks the passage of Solo-II float 8736, and the gray line marks the R/V *Reveille* acoustic Doppler current profiler transect with CTD stations indicated. (e) An area on the level top of NP shows small-scale relief and possible dead coral skeletons at 95 m depth. (f) NP's upper slope (110 m depth) exhibits some evidence of downslope scouring on rocky bottom. (g) A steep slope area at 120 m depth shows pitting and capture of small amounts of sediment. (h) A view at 150 m depth reveals heavy pitting of a rock surface with a deep crevice and a slope transitioning to an increasingly steep profile.

NP organisms are compared to those on the general outer reef/island slope of Palau from earlier observations and samples collected on over 100 scuba (Colin and Lindfield, 2019) and 75 submersible dives, principally with Deepworker 2000.

On November 22, 2016, currents at NP were measured from R/V *Roger Revelle* via the ship-mounted Teledyne RDI 150 kHz Ocean Surveyor acoustic Doppler current profiler (ADCP). Nineteen 300 m deep CTD casts were obtained over the submarine ridge on the eastern flank of NP with a Sea-Bird CTD (Figure 1d). Temperature measurements were collected at NP using temperature loggers mounted at 95 m depth (Onset U-22, 2010–2014, 1 hr interval; Sea-Bird Electronics 56, 2017–2019, 1 min interval) at 7°37.800'N, 134°40.150'E. Comparative temperature outer slope stations were located at Short Drop Off (SDO), 7°16.418'N, 134°31.440'E; on the eastern side of Babeldaob and Ulong Rock (ULR), 7°17.453'N, 134°14.442'E; on the western side of Babeldaob (see Figure 1a for locations). A SOLO-II float fortuitously transited the south past the eastern slope of NP in February 2019 (Figure 1d), profiling between the surface and 500 m depth while collecting temperature and salinity data on ascent and repeating the profile roughly every 140 minutes.

RESULTS

Geomorphology and Sedimentary Environment

NP is the elevated end of a ridge-like structure that extends over 1.6 km east from the shallow fringing reef slope of Ngarard State, eastern Babeldaob island (Figure 1a–d). The connecting ridge reaches about 150 m depth before rising to a minimum 92 m depth, where there is a flattened pinnacle. The low-relief pinnacle is covered with rocky features that extend only 10–40 cm above the surface along with small basins that have thin accumulations of sand (Figure 1e–h). The outer edges of the pinnacle slope to deeper water. Some crevices are found on the outer edge of the flattened top at ~100 m depth where we observed numerous fishes and invertebrates. It appears that the slope from about 110 m to 120 m is scoured with striations in the downslope direction (Figure 1f,g). At about 150 m, the rocky slope is densely pockmarked with small depressions (Figure 1h).

Temperature, Flow, and Vertical Profiles at NP

NP temperatures at 95 m depth exhibited different annual patterns from 2010 to 2019, registering major differences between the highest and lowest individual measurements each year (Figure 2). These temperatures closely tracked those of SDO and ULR, but NP temperatures 5 m deeper are slightly lower

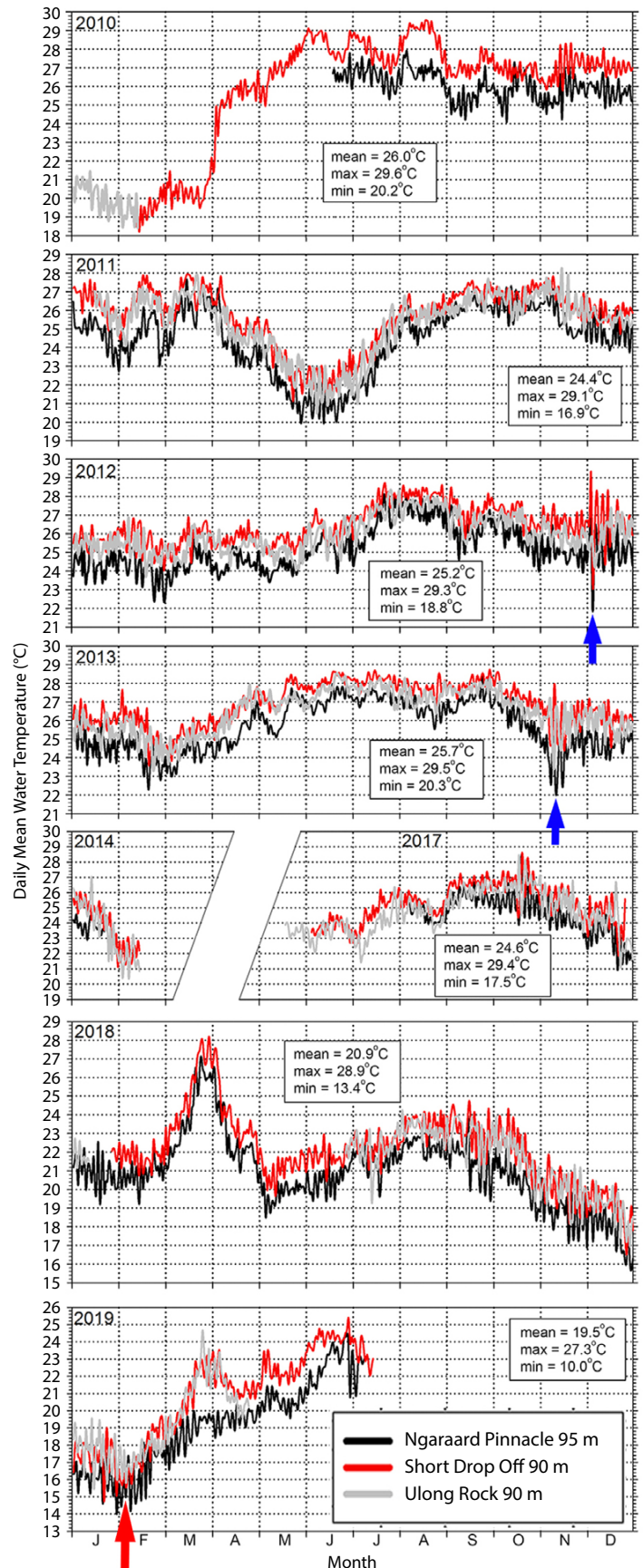


FIGURE 2. Hourly water temperatures (mid-2010 to 2014) and 30-minute means of 1-minute interval temperature data (2017–2019) from a temperature logger at Ngarard Pinnacle located at 95 m depth (black line), with comparison to 90 m depth at both Short Drop Off (red line) and Ulong Rock (gray line). The inset boxes show the yearly mean temperature at NP along with yearly maximum and minimum values of individual measurements at NP. Blue arrows indicate transits of super typhoons Bopha (2012) and Haiyan (2013) across Palau, and the red arrow indicates the period when temperatures reached levels associated with potential cold-water coral bleaching.

than the two 90 m stations on the main reef slope. For short periods (minutes to hours), temperatures at NP reached nearly 29°C or more each year (although records are incomplete for 2019), but daily mean values were much lower. Conversely, in early 2019, NP temperatures were very low, with specific measurements as low as 10°C and none higher than nearly 21°C (not shown), similar to other locations around Palau.

The 92 m deep top of NP and the adjacent submarine ridge are perpendicular to the coast of Babeldaob and the fringing reef (Figure 1a–d). The broad-scale incident westward flow of the North Equatorial Current is deflected northward or southward when it encoun-

ters Babeldaob. During the 2016 *Revelle* cruise at NP, the zonal velocity along a north-south track is smaller and eastward or offshore (Figure 3a), and the meridional velocity is stronger and northward in the upper 60 m, and southward below (Figure 3b). The vertical shear (change in meridional velocity with depth) is strongest between the two layers of flow, at around 75 m, which is near the top of the pinnacle (Figure 3c). The ship's CTD provides salinity and potential density (Figure 3d). The broadening of the isopycnal surfaces in the lee of NP (to the south) suggests that there may be some hydraulic blocking of the lower, southward flow, along with some mixing that reduces the stratification.

In February 2019, a SOLO-II profiling float moved with the prevailing southward flow past NP's eastern slope (see Figure 1d for the track), hitting bottom on a few dives over shallower topography (Figure 4). The thermocline, where temperature rapidly changes with depth, resides just above 100 m, coinciding with the apex of the pinnacle. Just below the thermocline, an area of weaker stratification is found in the lee of NP, as indicated in the 2016 *Revelle* CTD data (Figures 3 and 4). There is also a subsurface salinity maximum (Figures 3d and 4b) that is roughly 0.5 psu greater than the surface salinity.

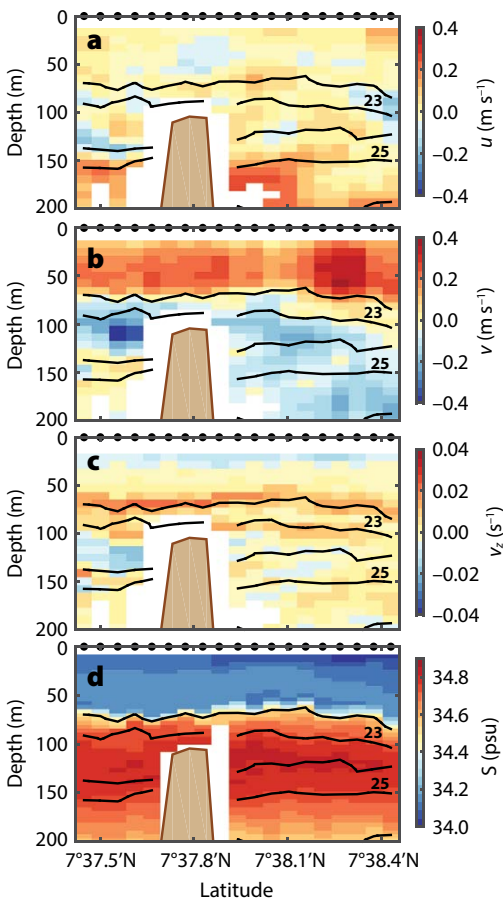


FIGURE 3. (a–c) Currents from R/V *Revelle*'s 150 kHz acoustic Doppler current profiler track indicated in Figure 1d (November 2016). (a) Zonal velocity (u) is eastward or offshore, and (b) meridional velocity (v) is northward in the upper 60 m and southward below. (c) Vertical shear (change in meridional velocity with depth) is greatest between the northward and southward flow. (d) Salinity and potential density from the ship's CTD (black contours at 1 kg m^{-3} intervals).

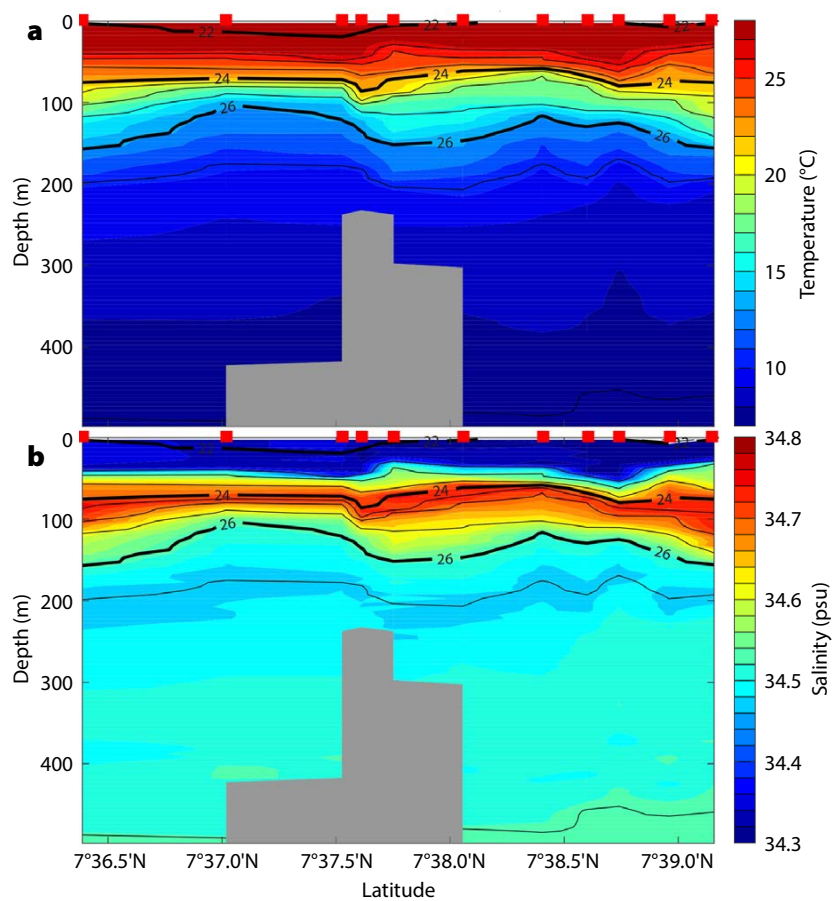


FIGURE 4. Sections of (a) temperature and (b) salinity from dives 130–140 of SOLO-II float 8736 transiting north to south past NP in February 2019, indicated on Figure 1d. Color shading indicates temperature and salinity, and black lines are isopycnals. Red squares along the top edges of the panels show the locations of profiles. The gray regions without color shading are where the float hit bottom on the NP ridge. Note the thermocline and the salinity maximum near 75 m depth.

Community Structure

NP's diverse and abundant faunal community is characterized by a variety of gorgonians (e.g., sea fans) and soft corals, a modest number of echinoderm species, and abundant and diverse bony fish fauna (62 species; **Table 1** includes relative abundance). Five species of macro-sponges were photographed (**Figure 5a–e**), including one stony sponge, *Microscleroderma herdmanni*. The only stony coral observed or collected was a small flattened species of *Leptoseris* (**Figure 5g**). Photo transects showed scattered small colonies of this species in a few areas, with coral cover much less than 1%. No branching or ahermatypic stony corals were observed. Interestingly, a few photographs (such as **Figure 1e**) show possible dead and biofouled coral colonies, and their provenance needs further examination.

A number of species of primnoid gorgonians were seen, and one species, *Callogorgia* cf. *elegans*, was collected. Several additional species of gorgonians, including a species of *Siphonogorgia* (collected) and two species of the soft coral genus *Eleutherobia* (collected), were seen in photos and video (**Figure 5f**). A zoanthid species with white polyps (**Figure 6a**), probably *Epizoanthus illoricatus* (Kise and Reimer, 2016), was found on dives and seen in drop-camera transects and was collected. Two possibly undescribed species of sea cucumbers were photographed (**Figure 6b,c**). Three or four species of sea urchins (tentatively identified as *Diadema clarkii*, *D. savignyi*, *Diadema* sp., and one undetermined), important herbivores on coral reefs (Muthiga and McClanahan, 2013), were photographed clustered together in groups of at least 10–20 mixed species individuals (**Figure 6e–h**; Gustav Paulay, Florida Museum of Natural History and Rich Mooi, California Academy of Sciences, pers. comm., November 28, 2019). A few unidentified crinoids were also seen.

NP has an abundant and diverse bony fish fauna (**Table 1**). On dives and photo transects, schools of planktivorous *Paracaesio xanthura* and *P. sordida* were seen above the pinnacle (**Figure 7c**). Associated with them were piscivorous *Caranx lugubris*, *C. melampygus*, and *Seriola dumerili* (**Figure 7a,b**), as well as lesser numbers of gray reef sharks (*Carcharhinus amblyrhynchus*) and silvertip sharks (*C. albimarginatus*). The low-relief bottom had clouds of anthines (Serranidae), particularly *Anthias parvirostris* (another zooplanktivorous fish), and other small reef fishes. Where there were more extensive crevices and cracks, large numbers of small to medium-sized reef fishes (<25 cm long) were seen (**Figure 7d,e**). The pinnacle was littered with many rubble mounds constructed by the tilefish *Hoplolatilus randalli* (similar to those described by Clark et al., 1998). No herbivorous reef fishes were observed.

Only a few plant species were observed at NP, including a leafy brown alga likely to be a species of *Distromium* (**Figure 6d**) and an unidentified finely branched green alga.

TABLE 1. Bony fishes observed on Ngarard Pinnacle from its shallowest depths at 92 m to a 120 m maximum. Qualitative abundance was documented from video recordings and designated as L = low (less than 15 individuals documented), M = medium (16–30 individuals), and H = high (31–100+ individuals).

Family	Taxa	Abundance
Acanthuridae	<i>Acanthurus xanthopterus</i>	L
	<i>Naso hexacanthus</i>	H
	<i>Naso lopezi</i>	L
Balistidae	<i>Odonus niger</i>	M
	<i>Sufflamen fraenatum</i>	L
	<i>Xanthichthys auromarginatus</i>	M
	<i>Xanthichthys caeruleolineatus</i>	L
Carangidae	<i>Carangoides plagiotaenia</i>	L
	<i>Caranx lugubris</i>	L
	<i>Caranx melampygus</i>	L
	<i>Elagatis bipinnulata</i>	L
Chaetodontidae	<i>Seriola dumerili</i>	L
	<i>Chaetodon burgessi</i>	L
	<i>Chaetodon guentheri</i>	L
	<i>Chaetodon kleinii</i>	L
Cirrhitidae	<i>Heniochus acuminatus</i>	L
	<i>Cyprinocirrhites polyactis</i>	L
Epinephelidae	<i>Cephalopholis aurantia</i>	L
	<i>Cephalopholis leopardus</i>	H
	<i>Cephalopholis sexmaculata</i>	L
	<i>Epinephelus retouti</i>	L
	<i>Gracila albomarginata</i>	L
Haemulidae	<i>Variola louti</i>	L
	Unknown spp.	L
	<i>Plectorhynchus picus</i>	L
	<i>Myripristis chryseres</i>	H
Holocentridae	<i>Neoniphon aurolineatus</i>	H
	<i>Sargocentron microstoma</i>	L
	<i>Bodianus bilunulatus</i>	L
Labridae	<i>Bodianus bimaculatus</i>	L
	<i>Bodianus neoperularis</i>	L
	<i>Bodianus sepiacaudus</i>	L
	<i>Cirrhilabrus earlei</i>	L
	<i>Labroides dimidiatus</i>	L
	Unknown spp.	L
Lethrinidae	<i>Wattsia mossambica</i>	L
	<i>Aphareus furca</i>	L
Lutjanidae	<i>Aphareus rutilans</i>	L
	<i>Lutjanus argentimaculatus</i>	H
	<i>Lutjanus quinquelineatus</i>	H
	<i>Lutjanus timorensis</i>	L
	<i>Paracaesio sordida</i>	H
Malacanthidae	<i>Paracaesio xanthura</i>	H
	<i>Hoplolatilus marcosi</i>	L
	<i>Hoplolatilus randalli</i>	H
	<i>Hoplolatilus starcki</i>	L
Pomacanthidae	<i>Apolemichthys trimaculatus</i>	L
	<i>Centropyge fisheri</i>	L
	<i>Centropyge heraldi</i>	L
Pomacentridae	<i>Genicanthus bellus</i>	L
	<i>Chromis analis</i>	L
Ptereleotridae	<i>Nemateleotris decora</i>	L
	<i>Nemateleotris helfrichi</i>	M
Scombridae	<i>Gymnosarda unicolor</i>	L
	<i>Holanthias borbonius</i>	H
	<i>Liopropoma latifasciatum</i>	H
Serranidae	<i>Luzonichthys seaver</i>	M
	<i>Pseudanthias fasciatus</i>	L
	<i>Pseudanthias flavoguttatus</i>	L
Symphysanodontidae	<i>Pseudanthias parvirostris</i>	H
	Unknown spp.	L
Tetraodontidae	<i>Canthigaster epilampra</i>	H

The putative *Distromium* sp. was common on hard surfaces in NP photographs, and it was sampled from rocks collected at 95 m depth. Numerous photographs also showed apparent encrusting coral-line algae, but no samples were obtained. No calcareous algae, common on Pacific deep reefs, were seen.

DISCUSSION

Investigations of lower mesophotic and rariphotic zones in the tropics have been limited due to their steep profiles and difficult working environments. Submersibles (Baldwin et al., 2018; Stefanoudis et al., 2019), remotely operated vehicles, multi-beam sonar, and autonomous underwater vehicles (Armstrong et al., 2019) have substantially increased knowledge of

the structure and communities of many deep habitats. However, scant attention has been directed at deep photic environments, such as our study site at NP, where connected shallow environments (altriphotic and upper mesophotic reefs) do not also occur. Looking at the worldwide scope of mesophotic reef environments (Loya et al., 2019), we found no comparable geomorphological counterparts to our Palau site in the western Pacific.

At 92 m depth, NP would generally be considered below the accepted limits of coral reef growth (60–75 m depth) in Palau. NP does not get detritus/organic matter from shallower depths, and it appears the community is based largely on zooplanktivory for its resident fish and invertebrate populations, with a minor

component of benthic primary production and herbivory also contributing.

Fluctuating temperatures at NP may preclude the establishment of a true mesophotic coral ecosystem and limit the occurrence of photophilic scleractinian corals. From 2010 to 2019, yearly mean temperatures at NP fluctuated between 20.9°C and 26°C on average (with a 2019 half-year mean of 19.5°C). The lowest values of any year are close to the lower limits for photophilic reefs (18°–20°C), while daily means were usually not below 20°C. However, during late 2018 to early 2019, temperatures were between 14°C and 20°C for five months. In addition, during El Niño periods, weekly/monthly mean temperatures at NP were at their lowest, while daily variation in temperatures

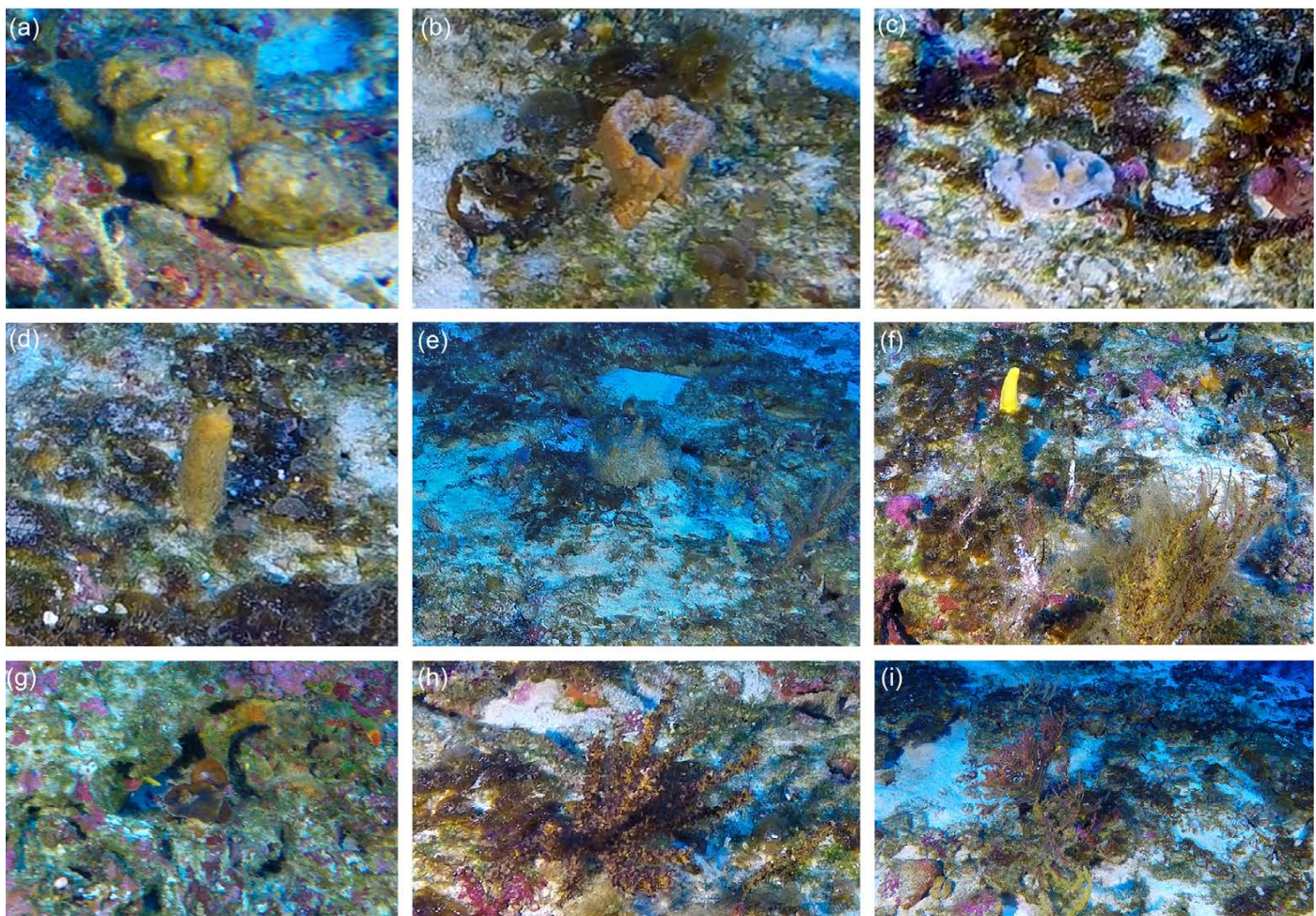


FIGURE 5. Organisms from Ngarard Pinnacle, 95–100 m depth. (a) Stony sponge *Microscleroderma herdmanni*. (b-d) Unidentified sponges. (e) Probable *Topsentia* sp. sponge. (f) Yellow soft coral *Eleutherobia* sp. at upper left with *Epizoanthus* sp. and unidentified hydroids in the foreground. (g) The flattened stony coral *Leptoseris* sp. is the only scleractinian seen or collected on NP. (h) Gorgonian or colony of *Epizoanthus* sp. (i) Gorgonian in area of mixed hard/sand bottom with cover of brown algae.

was high, changing as much as 10°–15°C over a few hours. Given these temperature minima and ranges, there is a high prospect for “cold water bleaching” of corals (Figure 2, red arrow), a poorly documented phenomenon that has been observed on Palau’s deep reefs (Colin and Lindfield, 2019).

NP is isolated from shallow sources that might supply sediment/talus downslope to affect the makeup of biological communities, and it is sufficiently deep that major sediment generators, such as calcareous algae, are not present. This is one of the unique and distinguishing characteristics of NP. The lack of material traveling downslope allows us to examine the structure of a reef that is supported largely by zooplankton transported by horizontal along-reef currents or rare events that result in downward supply of material from the surface. As the slopes on the edges of NP progressively steepen, evidence of downslope scouring by sediments can be seen (Figure 1f,g), except near 150 m. The presence of apparent erosional scouring on sloping rock surfaces at depth seems contradictory to the low potential for sediment production on the NP but may be indicative of strong currents impacting NP that provide forcing to erode surface over time despite low amounts of sedimentary materials.

The data from shipboard surveys and the Solo-II float transit provide a snapshot of the currents around NP and their potential role in the ecology of this deep reef system. Nutrient and water column biology were not sampled, so the tie between the flow dynamics and the support of the reef are speculative. However, large directional shifts in the currents flowing above the pinnacle can impact NP and its bottom communities. Similar current shifts at depths of 60–80 m observed on two of five scuba dives required aborting of those dives. Typical of this region of the western Pacific, there is a salinity maximum at the depth of the thermocline (Schönau and Rudnick, 2015, 2017). As the ridge is located at the region of maximum stratification, internal waves and

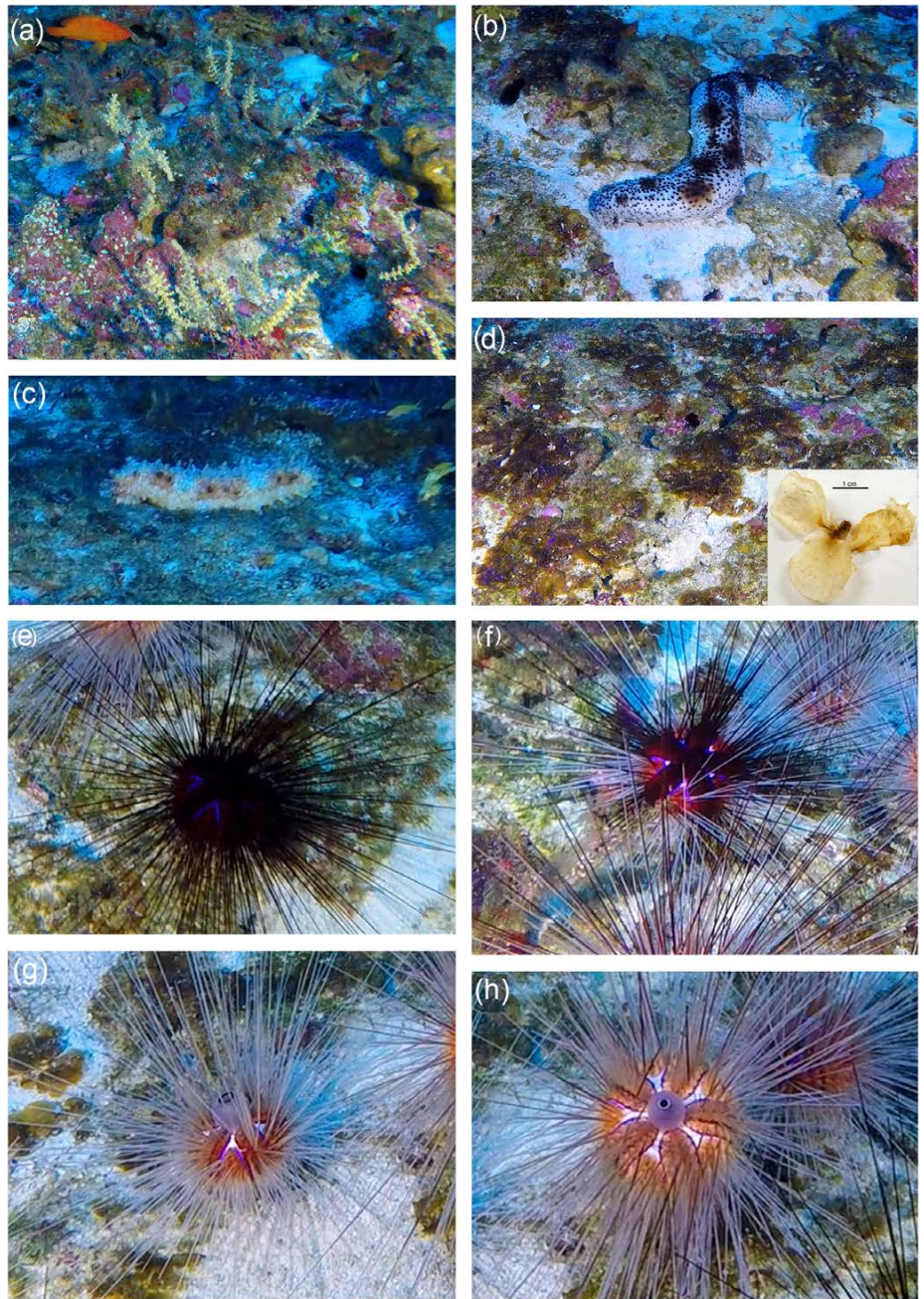


FIGURE 6. Organisms from Ngaraard Pinnacle, 95–100 m depth. (a) Mixed hard and sand bottom with *Epizoanthus illoricatus* and leafy brown algae (likely a *Distromium* sp.) on rock. A small grouper *Cephalopholus aurantius* is present at upper left. (b) Sea cucumber *Holothuria* sp. (c) Sea cucumber *Stichopus* sp. (d) Area of rock with brown alga, probably *Distromium* sp., on it. Inset: Detail of alcohol-preserved piece of likely *Distromium* sp. (e) Sea urchin *Diadema savignyi*. (f) Diademnid sea urchin, identification uncertain. (g) Sea urchin, likely *Diadema clarkii*. (h) Another probable individual of *D. clarkii*.

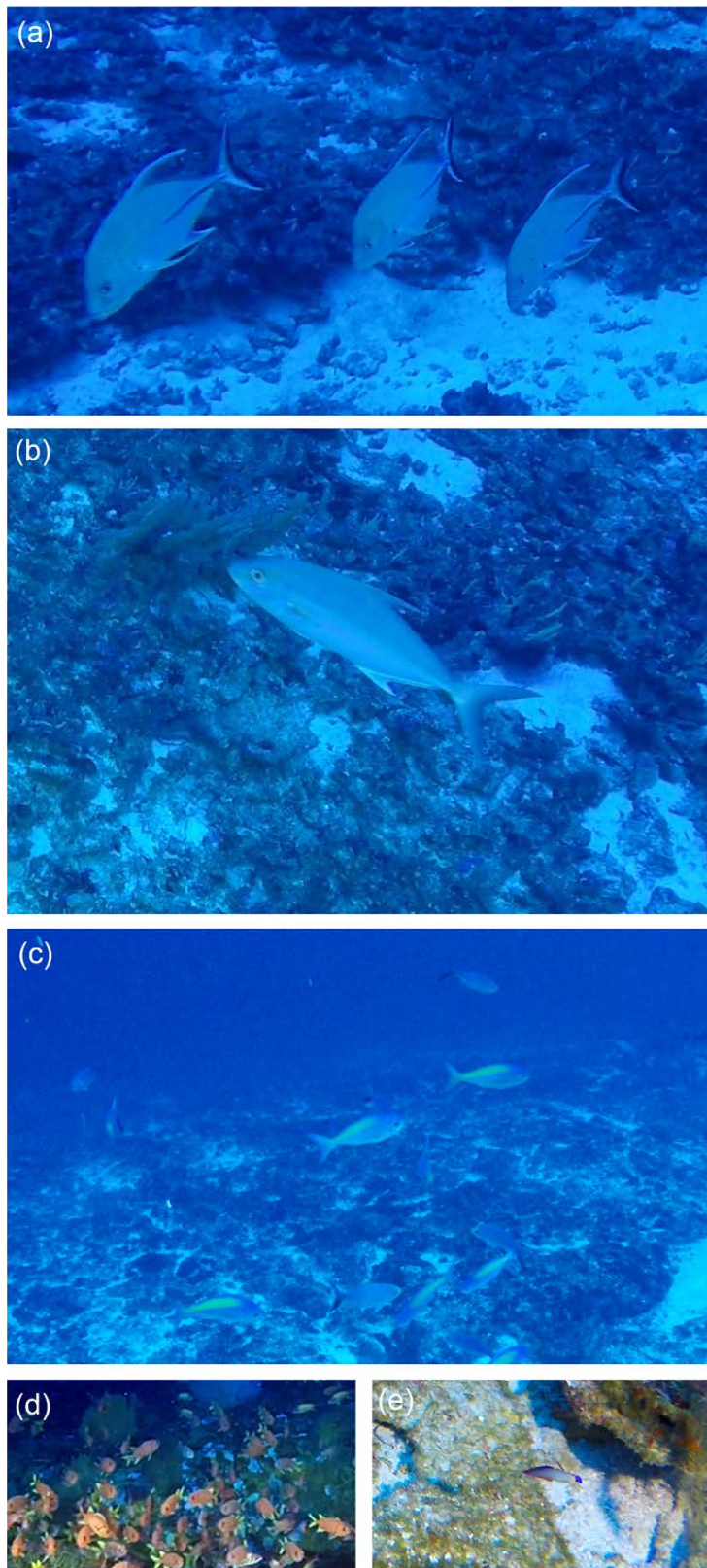


FIGURE 7. Fishes observed on Ngarard Pinnacle, 95–100 m depth. (a) The common predator *Caranx lugubris* swims above the pinnacle in small groups. (b) *Seriola dumerili* is another predatory species on NP. (c) The caesionids *Paracaesio sordida* and *P. xanthura* occur as a cloud of individuals above the pinnacle. (d) In areas with crevices, large numbers of *Myripristis chryseres* and other reefs fishes can occur. (e) The small eleotrid *Nemateleotris decora* is a strictly mesophotic species found on the pinnacle.

changes in sea surface height from annual and interannual variability likely force the thermocline up and down, creating the large salinity and temperature fluctuations that impact the biological community.

CONCLUSIONS

While many aspects of coral reef ecology are becoming increasingly well known, knowledge of deeper environments, those termed mesophotic and rariphotic, is still relatively poor. There are few examples of isolated hard bottom areas that rise from depths below which coral reefs usually do not exist to provide a perspective of what a “reef” would look like when deprived of sediment and organic materials derived from shallow habitats. NP is one such example, and it has proven to have a community structure supported principally by zooplanktivory (based on the numbers of zooplanktivorous fishes occurring there). The only herbivores confirmed from the site are sea urchins, which may be grazing a small population of benthic algae (Steneck et al., 2017). The fish fauna consisted of either shallow water species ranging downward near their lower depth limits or species from shallow reef genera and families that occur only at mesophotic depths. Reef invertebrates were of limited diversity, with only one species of stony coral, and the overall community could not be considered a “coral reef.”

Currents and water temperature over the pinnacle are dynamic. At times, there is current shear in the water column above NP, with the shallow and deeper flows running opposite to one another. Along the pinnacle ridge, there are also sharp temperature changes with depth, with large extremes occurring during El Niño. Temperature monitoring over five years indicates long periods when temperatures were below those associated with photophilic coral reefs. The NP community provides supporting evidence that temperature limits the depth of mesophotic reefs in Palau. The lack of an upslope source of biological material and sediments makes NP an isolated island of bottom habitat. The scoured surfaces of NP indicate the potential presence of dynamic currents that likely play an important role in supporting the ecology of NP. ©

REFERENCES

- Armstrong, R., O. Pizarro, and C. Roman. 2019. Underwater robotic technology for imaging mesophotic coral. Pp. 973–988 in *Mesophotic Coral Ecosystems*. Y. Loya, K.A. Puglise, and T.C.L. Bridge, eds. Coral Reefs of the World, vol. 12, Springer, Cham, https://doi.org/10.1007/978-3-319-92735-0_51.
- Baker, E.K., P.T. Harris, and K. Puglise, eds. 2016. *Mesophotic Coral Ecosystems: A Lifeboat for Coral Reefs?* United Nations Environment Programme and GRID-Arendal, 86 pp.
- Baldwin, C.C., L. Tornabene, and D.R. Robertson. 2018. Below the mesophotic. *Scientific Reports* 8(1):4920, <https://doi.org/10.1038/s41598-018-23067-1>.
- Bongaerts, P., and T.X. Smith. 2019. Beyond the “deep reef refuge” hypothesis: A conceptual framework to characterize persistence at depth. Pp. 881–895 in *Mesophotic Coral Ecosystems*. Y. Loya, K.A. Puglise, and T.C.L. Bridge, eds. Coral Reefs of the World, vol. 12, Springer, Cham, https://doi.org/10.1007/978-3-319-92735-0_45.
- Clark, E., J.F. Pohle, and B. Halstead. 1998. Ecology and behavior of tilefishes, *Hoplostilus starcki*, *H. fronticinctus* and related species (Malacanthidae): Non-mound and mound builders. *Environmental Biology of Fishes* 52(4):395–417, <https://doi.org/10.1023/A:1007440719123>.
- Colin, P.L. 2018. Ocean warming and the reefs of Palau. *Oceanography* 31(2):126–135, <https://doi.org/10.5670/oceanog.2018.214>.
- Colin, P.L., and S.J. Lindfield. 2019. Palau. Pp. 285–299 in *Mesophotic Coral Ecosystems*. Y. Loya, K.A. Puglise, and T.C.L. Bridge, eds. Coral Reefs of the World, vol. 12, Springer, Cham, https://doi.org/10.1007/978-3-319-92735-0_16.
- Hammer, W.M., and J.L. Largier. 2012. Oceanography of the planktonic stages of aggregation spawning reef fishes. Pp. 159–190 in *Reef Fish Spawning Aggregations: Biology, Research and Management*. Y.J. Sadovy de Mitcheson and P.L. Colin, eds. Springer, Dordrecht.
- Kise, H., and J.D. Reimer. 2016. Unexpected diversity and a new species of *Epizoanthus* (Anthozoa, Hexacorallia) attached to eunicid worm tubes from the Pacific Ocean. *ZooKeys* 562:49–71, <https://doi.org/10.3897/zookeys.562.6181>.
- Lowe, R.J., and J.L. Falter. 2015. Oceanic forcing of coral reefs. *Annual Review of Marine Science* 7:43–66, <https://doi.org/10.1146/annurev-marine-010814-015834>.
- Loya, Y., K.A. Puglise, and T.C.L. Bridge, eds. 2019. *Mesophotic Coral Ecosystems*. Coral Reefs of the World, vol. 12, Springer, Cham, <https://doi.org/10.1007/978-3-319-92735-0>.
- Monismith, S.G. 2007. Hydrodynamics of coral reefs. *Annual Review of Fluid Mechanics* 39:37–55, <https://doi.org/10.1146/annurev.fluid.38.050304.092125>.
- Muthiga, N.A., and T.R. McClanahan. 2013. Diadema. Pp. 257–274 in *Developments in Aquaculture and Fisheries Science*, vol. 38, Elsevier.
- Schönau, M.C., and D.L. Rudnick. 2015. Glider observations of the North Equatorial Current in the western tropical Pacific. *Journal of Geophysical Research* 120:3,586–3,605, <https://doi.org/10.1002/2014JC010595>.
- Schönau, M.C., and D.L. Rudnick. 2017. Mindanao Current and Undercurrent: Thermohaline structure and transport from repeat glider observations. *Journal of Physical Oceanography* 47:2,055–2,075, <https://doi.org/10.1175/JPO-D-16-0274.1>.
- Spalding, H.L., J.M. Copus, B.W. Bowen, R.K. Kosaki, K. Longenecker, A.D. Montgomery, J.L. Padilla-Gamiño, F.A. Parrish, M.S. Roth, S.J. Rowley, and others. 2019. The Hawaiian archipelago. Pp. 445–464 in *Mesophotic Coral Ecosystems*. Y. Loya, K.A. Puglise, and T.C.L. Bridge, eds. Coral Reefs of the World, vol. 12, Springer, Cham, https://doi.org/10.1007/978-3-319-92735-0_25.
- Stefanoudis, P.V., E. Gress, J.M. Pitt, S.R. Smith, T. Kincaid, M. Rivers, D. Andradi-Brown, G. Rowlands, L.C. Woodall, and A.D. Rogers. 2019. Depth-dependent structuring of reef fish assemblages from the shallows to the rariphotic zone. *Frontiers in Marine Science*. 6:307, <https://doi.org/10.3389/fmars.2019.00307>.
- Steneck, R.S., D.R. Bellwood, and M.E. Hay. 2017. Herbivory in the marine realm. *Current Biology* 27(11):R484–R489, <https://doi.org/10.1016/j.cub.2017.04.021>.

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AUTHORS

Patrick L. Colin (crrfpalau@gmail.com) is Director, Coral Reef Research Foundation, Koror, Palau. **T.M. Shaun Johnston** is Associate Research Oceanographer, **Jennifer A. MacKinnon** is Professor and Associate Dean, **Celia Y. Ou** is a PhD candidate, **Daniel L. Rudnick** is Professor, **Eric J. Terrill** is Director, Coastal Observing Research and Development Center, all at Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA. **Steven J. Lindfield** is Research Biologist, Coral Reef Research Foundation, Koror, Palau. **Heidi Batchelor** is Programmer/Analyst, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA.

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