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Submerged reef features in Apo and Tubbataha Reefs, Philippines, revealed paleo sea‑level history during the last deglaciation

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Abstract

The morphology of coral reefs provides an efective benchmark of past sea levels because of their limited vertical range of formation and good geologic preservation. In this study, we analyze the seafoor morphology around two atolls in the Philippines: Tubbataha Reef, in Palawan, and Apo Reef, in Occidental Mindoro. High-resolution multibeam bathymetry to a depth of 200 m reveals seafoor features including reef ridges and staircase-like terraces and scarps. Depth profles across the reefs show terraces formed within six and seven depth ranges in Tubbataha Reef and in Apo Reef, respectively. These were further observed through a remotely operated vehicle. The terraces and scarps are interpreted as backstepping reefs that were drowned during an overall rise in sea level from the Last Glacial Maximum (LGM). Terraces are used as indicators of paleo sea level and the separation between terraces as the magnitude of sea-level rises coeval with meltwater pulse events during the last deglaciation. The pattern for both Apo and Tubbataha reefs indicates subsidence, consistent with the absence of Holocene emergent features and their atoll morphologies. Subsidence of up to 17 m since the LGM in Apo Reef is mainly attributed to the downbowing of the crust toward Manila Trench. In Tubbataha Reef, subsidence of up to 14 m is attributed to the continuous cooling of the volcanic crust underlying the atoll. These can be used to fll gaps in the tectonic history of the study sites from the last deglaciation.

Introduction

Coral reefs are the largest biologically constructed features on the seafoor and are characterized by their complex structure and ecology (Wood [1999\)](#page-17-0). Their morphologies provide signifcant evidence for past sea levels due to their limited vertical range, high potential for preservation, and suitability for dating (Lighty et al. [1982](#page-15-0); Stoddart [1990](#page-17-1); Woodroffe [2008](#page-17-2); Woodrofe & Webster [2014\)](#page-17-3). Reef morphology is a product of changing sea levels as well as the physical and ecological conditions during its formation (Lutzenkirchen et al. [2023,](#page-16-0) Montaggioni [2005;](#page-16-1) Smith and Buddemeier; [1992](#page-16-2); Stoddart; [1969](#page-17-4); Woodroffe and Webster [2014\)](#page-17-3).

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Models by Neumann and Macintyre ([1985\)](#page-16-3) and Davies and Montaggioni ([1985\)](#page-14-0) outline how reef growth responds to the availability of accommodation space and can be altered by sea-level fuctuations. Reefs may be able to vertically "keep up" if accretion rates are roughly equal to the rate of sea-level rise. Reefs may not initially keep pace with sealevel rise, but deep reef communities can be progressively replaced by shallow water forms and "catch up" with sea level. Reefs drown when reef accretion is inhibited as it signifcantly lags with the rise of sea level (Blanchon and Shaw [1995\)](#page-14-1) and backstep when there is an available landward substrate behind to retreat into (Hubbard et al. [1997](#page-15-1)). Reefs emerge when relative sea level drops, exposing reef sections to the surface (Dickinson [2001](#page-14-2)). During prolonged sea-level stability, shallow reefs are forced to grow horizontally toward the available seaward space. Extensive horizontal reef surfaces provide vertical reference points for the upper growth limit of coral reefs during this period (Kennedy and Woodrofe [2002](#page-15-2); Montaggioni [2005](#page-16-1)). Antecedent substrates and exposed reefs are subject to erosion by wave action (Grigg et al. [2002](#page-15-3)). This mechanism etches wave-cut platforms and marine notches close to sea level and produces

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a sea cliff landward (Kershaw and Guo [2001](#page-15-4)). Over time, multiple reef terraces indicate the number of interstadial sea-level events in a region (Woodroffe and Webster [2014](#page-17-3)). Combined with the vertical effect of tectonics, coral reefs are used to determine the relative sea-level (RSL) history (Woodroffe and Webster [2014](#page-17-3)).

Eustatic sea levels have risen by around 120 m since the Last Glacial Maximum (LGM) (Fairbanks [1989](#page-14-3); Yokoyama et al. [2001;](#page-17-5) Hanebuth et al. [2000;](#page-15-5) Peltier [2002;](#page-16-4) Clark and Tarasov [2014;](#page-14-4) Austermann et al. [2013](#page-14-5); Lambeck et al. [2014](#page-15-6); Gowan et al. [2021](#page-15-7)). The rise of sea level has not been uniform, having episodes of relative stability during stillstands which are separated by rapid rises (Bard et al. [1996](#page-14-6); Fairbanks [1989\)](#page-14-3). Rapid rises in sea level are commonly attributed to meltwater pulses (MWP) associated with rapid ice melting or ice sheet collapses in high latitudes (Blanchon and Shaw [1995;](#page-14-1) Fairbanks et al. [1992](#page-14-7); Harrison et al. [2019](#page-15-8)). During these pulses, sea levels have risen by as much as 60 mm/year based on submerged reef terraces and stacked delta records (Fairbanks [1989;](#page-14-3) Blanchon and Shaw [1995](#page-14-1); Peltier [2002;](#page-16-4) Liu and Milliman [2004](#page-15-9); Clark et al. [2004](#page-14-8); Deschamps et al. [2012;](#page-14-9) Lin et al., [2021](#page-15-10); Abdul et al. [2016](#page-14-10); Harrison et al. [2019](#page-15-8); Brendryen et al. [2020](#page-14-11)). In the Philippines, sea-level reconstructions during the Holocene are based on dated coastal reef terraces, mangrove deposits, tidal notches, and borehole data with age dates younger than 10.2 ka in Palawan, Bohol, Samar, and Ilocos (Berdin et al. [2003;](#page-14-12) Maeda et al. [2004;](#page-16-5) Omura et al. [2004;](#page-16-6) Ringor et al. [2004;](#page-16-7) Shen et al. [2010](#page-16-8); Siringan et al. [2016\)](#page-16-9). These records are based on emergent structures that refect the Holocene sea-level highstand and uplift. Sea-level records in emergent reefs and tidal notches in northern Luzon and Palawan indicate three highstands (7.5–6.0 ka, 6.0–4.0 ka, and 2.8–1.2 ka) in the mid-Holocene some of which occur as high as 4.2 m (Maeda et al. [2009;](#page-16-10) Maeda and Siringan [2004](#page-16-11)). These deglacial sea-level trends were very similar to records from Abrolhos Island, Australia, and higher than the paleo sea-level records in Tahiti (Shen et al. [2010;](#page-16-8) Siringan et al. [2016](#page-16-9)). Higher than present paleo sea-level markers in Pangasinan, Davao, and Ilocos have also been attributed to co-seismic uplift events during the Holocene (Maxwell et al. [2018](#page-16-12); Ramos et al. [2012](#page-16-13); Ramos and Tsutsumi [2010\)](#page-16-14). Reef terraces during the deglacial period up to a depth of 120 m were also mapped on Pag-asa Island (Janer et al. [2023](#page-15-11)). Higher than present paleo sea-level indicators towards 131 ka MIS-5e and 237 ka MIS-7 were also identifed in Bohol and Palawan (Omura et al. [2004;](#page-16-6) Ringor et al. [2004](#page-16-7)).

The advent of high-resolution acoustic mapping allowed new insights into describing submerged reefs, which were formed during periods of lower than present sea level, at larger extents and high resolutions (Beaman et al. [2008](#page-14-13); Grigg et al. [2002;](#page-15-3) Khanna et al. [2017\)](#page-15-12). High-resolution multibeam echosounder surveys yield bathymetric data that can image fne-scale and laterally extensive morphological features on the seafoor including reef terraces (i.e., Abbey et al., [2011;](#page-14-14) Beaman et al. [2008;](#page-14-13) Conway et al. [2005;](#page-14-15) Gomes et al. [2020;](#page-14-16) Kan et al. [2015](#page-15-13); Khanna et al. [2017](#page-15-12); Kim et al. [2013;](#page-15-14) Lebrec et al. [2022;](#page-15-15) de Silveira et al. [2020](#page-14-17); Storlazzi et al. [2003](#page-17-6); Tibor et al. [2010;](#page-17-7) Varzi et al. [2023](#page-17-8); Vieira et al. [2023;](#page-17-9) Zecchin et al., [2015](#page-17-10)). Past studies in Hawaii (Grigg et al. [2002](#page-15-3)), Maldives (Fürstenau et al. [2010](#page-14-18); Rovere et al. [2018\)](#page-16-15), Australia (Abbey et al. [2011;](#page-14-14) Beaman et al. [2008](#page-14-13); Lebrec et al. [2022\)](#page-15-15), Gulf of Mexico (Khanna et al. [2017](#page-15-12)), Mediterranean Sea (Zecchin et al. [2015](#page-17-10)), Ryukyus, Japan (Inoue and Arai [2020\)](#page-15-16), Rio Grande do Norte, Brazil (Gomes et al. [2020\)](#page-14-16), and Abrolhos Shelf, Brazil (Vieira et al. [2023](#page-17-9)), have shown that the morphology of submerged reef terraces can provide regional interpretation of the origins and development of reefs even in the absence of age-dated materials.

In this study, high-resolution multibeam echosounder data along with remotely operated vehicle observations were acquired along the upper slopes of Apo and Tubbataha Reef, in the Philippines, down to a depth of 200 m, to identify and describe submerged coral reef terraces and ridges. The study aims to identify and describe submerged features of coral reefs from the bathymetric data. This can give insights into how coral reefs in the archipelago have responded in the past and their resilience to future sea-level changes. Recognizing the nature of past sea-level rises during deglaciation is critical for informing predictions on the future vertical behavior of global oceans. This study can also be used to further understand the neotectonic movements of the study sites since the LGM.

Regional setting

Apo Reef (12.67° N, 120.46° E) is located in Mindoro Strait, about 40 km west of Mindoro Island, Philippines. On the other hand, Tubbataha Reef (8.89° N, 119.73° E) is located in the middle of the Sulu Sea, about 160 km southeast of Palawan Island, Philippines (Fig. [1](#page-2-0)). Regionally, both are located around the Palawan microcontinent (PMC), a margin of the Sundaland-Eurasia plate that converges toward the Philippine Sea Plate (PSP) (Aurelio [2000](#page-14-19)). PMC converges to the western side of the Philippine Mobile Belt, an active region that accommodates subduction from opposing polarities due to the convergence with PSP (Aurelio [2000](#page-14-19)) (Fig. [1](#page-2-0)).

Apo Reef

Apo Reef is an offshore atoll found off the western coast of Mindoro Island (Fig. [1\)](#page-2-0). The main reef body rises from a depth greater than 1000 m (Glenn-Sullivan and Evans [2001](#page-14-20)). The atoll consists of two sub-triangular reefs, on the northern and southern atolls (Bacabac et al. [2023\)](#page-14-21).

Fig. 1 Location of Apo Reef and Tubbataha Reef within the tectonic framework of the Philippines. Crustal boundaries are based on structural studies on the South China Sea and the Philippines by Aurelio et al. (2014) (2014) , Franke et al. (2014) , and Pubellier et al. (2018) (2018) . The green line represents the position of the cross-section. (B) Schematic cross-section of the tectonic settings of Tubbataha Reef and

Apo Reef. These were adapted from the studies by Hall et al. [\(1995](#page-15-18)), Li et al. [\(2014](#page-15-19)), Rangin et al. [\(1988](#page-16-16)), and Rangin and Silver [\(1991](#page-16-20)). Abbreviations: SCS=South China Sea plate, PSCS=proto-South China Sea plate, CdSR=Cagayan de Sulu Ridge, MS=Mindoro Strait

Apo Reef is built on a small submarine platform (Zacher [1981](#page-17-11)) within the Palawan-Reed Bank Continental platform, in the back-arc region of the southern end of Manila Trench. Manila Trench is an active east-dipping subduction zone that subducts the South China Sea plate toward Luzon Island (Aurelio [2000;](#page-14-19) Hayes and Lewis, [1984\)](#page-15-17). The southern termination of the trench is characterized by a complex tectonic fabric formed between an arc-trench gap (Rangin et al. [1988](#page-16-16)). Onshore, north of Mindoro, is a transpressive region composed of parallel folds and thrust faults (Faure et al. [1989;](#page-14-22) Marchadier and Rangin [1990;](#page-16-17) Sarewitz and Karig [1986](#page-16-18)). Busuanga Island, on the south, is part of a stable continental fragment that has accreted since the Mesozoic (Zamoras and Matsuoka [2004](#page-17-12)). Ofshore areas in North Palawan are underlain by the platform carbonates of Nido Limestone which started to formed during the Oligocene to Miocene (Steuer et al. [2013\)](#page-17-13).

Apo Reef is located in the middle of Mindoro Strait, which connects the Sulu Sea and the South China Sea. The surface wind patterns in the study sites are impacted by the

East Asian Monsoon System (Pullen et al. [2011](#page-16-21)). In winter, they predominantly blow from the northeast, while in summer, they shift to southwesterly directions. During transitional periods, the wind patterns become highly unpredictable (Wyrtki, [1961\)](#page-17-14). Mindoro Strait is predominated by a southward current that provides infow to the Sulu Sea and is subject to anomalous northerly surges of reversals and cyclonic eddies during monsoon transitions (Hurlburt et al. [2011](#page-15-20); Pullen et al. [2011\)](#page-16-21).

Tubbataha Reef

Tubbataha Reef is an ofshore atoll complex covering three reef atolls in the middle of the Sulu Sea (Fig. [1\)](#page-2-0). The study site covers the north atoll of Tubbataha Reef. Two islets are located at the north (Bird Islet) and south (Ranger Station) ends of the north atoll (White and Palaganas [1991](#page-17-15)). Tubbataha Reef is among the reefs found on the southwestnortheast-oriented Cagayan Ridge across the Sulu Sea (Ledesma [2001](#page-15-21)).

Cagayan Ridge, also known as Cagayan de Sulu Ridge, is a remnant island arc associated with the ancient subduction of the proto-South China Sea along the Palawan Trough (Rangin et al. [1990\)](#page-16-22). The onset of the volcanism started during the Oligocene-Early Miocene and ended during the Middle Miocene (Rangin and Silver [1991\)](#page-16-20). The cessation of its volcanism is associated with the docking of the Palawan-Reed Continental Platform toward the Sulu Basin (Rangin and Silver [1991](#page-16-20)). Cagayan Ridge is capped by up to 400-m-thick coralgal reef deposits that have been deposited since the Middle Miocene (Kudrass et al. [1990](#page-15-22); Rangin and Silver [1991](#page-16-20)). This observation alongside dredged coral samples in Sibutu Passage at more than 500 m depth indicates that the reefs along the Cagayan Ridge have undergone significant subsidence (Krause [1966\)](#page-15-23). Surface currents in the Sulu Sea exhibit seasonal changes coinciding with the monsoon system. In summer, currents predominantly originate from the south, while during winter, they form counterclock-wise gyres (Wang et al. [2006\)](#page-17-16).

Methods

Multibeam echosounder survey

High-resolution bathymetry was collected using an R2Sonic 2022 multibeam echosounder system mounted on the side of an outrigger boat. Surveys on Apo Reef were conducted on May 27–29, 2015, and March 12–17, 2016, and those on Tubbataha Reef North Atoll (TRNA) on April 4 and 5, 2016. The multibeam echosounder system was set at a frequency between 200 and 400 kHz with a maximum swath coverage of 160 $^{\circ}$, with beam widths of $1^{\circ} \times 1^{\circ}$ at 400 kHz and $2^{\circ} \times 2^{\circ}$ at 200 kHz. A conductivity, temperature, and depth (CTD) profiler was deployed daily to determine the sound velocity change in the water column within the survey area covered. Surveys were done at a speed of 3–5 knots, following the isobath of each site. The minimum depth that was surveyed is at \sim 5 m to avoid possible damage to the survey boat, and thus, the modern reef fat was not covered. The maximum depth of the surveys was set at 200 m. A frequency of 400 kHz was used for depths of 0–100 m and 200 kHz for depths between 100 and 200 m. Raw bathymetric data were post-processed using HYPACK and HYSWEEP software. Instrument setup measurements, tide level corrections, and CTD profle corrections were integrated with the raw data during this process. Harmonic tides from WXTide32 during the period of the survey were incorporated in the correction. Tidal range from the closest tide stations in Apo Reef is at 1.03 m and Tubbataha is at 1.4 m (NAMRIA [2022\)](#page-16-23). Total propagated uncertainty for vertical depth measurements was determined at 18 cm. Grid models were then generated using HYPACK CUBE (combined uncertainty and bathymetric estimator) fltering and gridding algorithm (Calder and Mayer [2003](#page-14-25)) at a nominal spacing of 5 m for interpretation of geomorphology and to account for GNSS positioning errors. Bathymetric data were gathered around each atoll in Apo Reef. The northeastern edge of the North Atoll was not surveyed due to poor accessibility from the base station on Apo Island. The channel separating the North Atoll and South Atoll was also covered. For Tubbataha Reef, sections within the west and east of the north atoll were covered. Covering the whole extent of TRNA was not possible due to time constraints.

Terraces were analyzed for their continuity by observing and manually tracing the change of curvature or slope breaks computed in the bathymetric data. This was done by inspecting corresponding bathymetry, slope, and curvature. Profles were also extracted every 100 m in a downslope direction to aid in identifying terraces. Terrace values from the bathymetric profles were measured at the base of the terrace. When the terrace base is not well defned, it is represented by the point where the curvature is at maximum value between the terrace and scarp. This ensures that the depth represents the least amount of vertical sedimentation. Terraces were also scrutinized for their continuity within the reef body. Hypsograms were computed from the gridded bathymetric data. Flatter reef surfaces are represented as peaks in the hypsogram that correspond to broad features in a reef. Terrace continuity and hypsograms were used to estimate the range of depths of each terrace (Harris et al. [2008](#page-15-24)). Depth ranges are determined by the minimum and maximum depth determined for each terrace. Descriptions of mapped reef features follow the defnitions

of the International Hydrographic Organization for naming undersea features. Slopes were described in this paper using the following modifiers: flat $(0-5^{\circ})$, gentle $(5-30^{\circ})$, steep $(30-60^{\circ})$, and sub-vertical $(80-90^{\circ})$.

In the absence of age-dated materials, we use sea-level records from the West Pacifc to reference the age of the submerged reef terraces. The derived terrace depths from the bathymetric data are compared to deglacial sea-level reconstructions from the Yellow River Delta (Liu et al. [2004\)](#page-15-25) and Sunda Shelf (Hanebuth et al. [2011](#page-15-26); Shaw et al. [2023\)](#page-16-24). Yellow River Delta and Sunda Shelf sea-level records were gathered from transgressive sequences along passive margins. Coral reef records in the West Pacifc were also included to reference reef formation during the last deglacial. This includes data from Tahiti (Bard et al. [1996\)](#page-14-6) and Huon Peninsula (Ota and Chappell [1999](#page-16-25)). These records provide the most proximal and complete reconstructions of sea level in the past 19,000 years. Sealevel records in the Philippines that span the past 10.2 ka (Maeda et al. [2009](#page-16-10), [2004](#page-16-5); Shen et al. [2010](#page-16-8); Siringan et al. [2016](#page-16-9)) provide information on higher than present sea-level stands.

Underwater camera observation

A remotely operated vehicle (ROV) was deployed to document the nature of the reef substrate. Action cameras were attached to the ROV to retrieve high-resolution images aside from the video footage from the ROV. The ROV was driven close to the corals, seafoor, walls, and other reef structures to allow identifcation of reef features. Video footages retrieved from the ROV and the action cameras were analyzed for the presence of corals and the character of the substrate. Three sites for ROV deployment were done in Apo Reef, and two sites were done for Tubbataha Reef (Table [1\)](#page-4-0).

Table 1 Deployment sites for remotely operated vehicle (ROV) surveys

Site	Location	Maximum depth surveyed
Apo Reef		
Apo Island	12.6530° N, 120.4199° E	149 _m
North Atoll	12.7355° N, 120.4622° E	78 m
South Atoll	12.6352° N, 120.4549° E	80 m
Tubbataha Reef North Atoll		
East side (Malayan site)	8.8844° N, 119.8850° E	156 m
West side (shark point)	8.9345 \degree N, 120.0081 \degree E	120 m

Results

Apo Reef

Apo Reef is separated into three areas: Apo Reef North Atoll (ARNA), Apo Reef South Atoll (ARSA), and Apo Island (Fig. [2](#page-5-0)). Small coral limestone outcrops occur within the reefs: Cayos del Bajo (locally named Tinangkapan Island), a 100-m-wide outcropping rock within the ARNA, and Apo Menor Island (locally named Binanggaan Island), a 250-m-wide outcropping rock within the western portion of the South Atoll. To the west, Apo Island is a separate structure, wherein a 500 m sandy beach has accumulated around a limestone outcrop (Fig. [3\)](#page-6-0). The surfaces of the limestones are highly karstifed. Limestone exposures are observed as massive, gray-white, nonporous, and crystalline. These limestone outcrops are well cemented and indurated. Tidal notches above present levels are also absent in the outcrops.

Figure [2](#page-5-0) shows the distribution and horizontal continuity of the terrace edges traced from the bathymetric model. The morphology of each reef varies. Both the ARNA and Apo Island have very predominantly steep slopes around them (Fig. [4](#page-6-1)). In contrast, the South Atoll has a gentle slope on its southeastern side. Notably, the rims of all three reefs have multiple, continuous paired terraces and scarps. The depths covered by the terraces are summarized in Table [2.](#page-6-2)

Apo Island

Four continuous terraces were mapped around Apo Island. Terraces at the northwest and southeast sides are wider. The shallowest surveyed terraces on Apo Island occur at A1, 7 ± 1 m, and A2, 14.5 ± 3.5 (Fig. [5](#page-7-0)). Spur and groove structures on the island are closely spaced and typically over a 100 m long, running obliquely around the island and terminate below A1. The upper reef terraces at A1 are dominated by branching and tabulate *Acropora*, with a few columnar and encrusting corals and crinoids. The gentle drop-off is covered by similar branching and tabulate corals. The rubble-flled ledges are mostly tabulate and encrusting coral colonies and a few branching *Acropora*. Dense and diverse clusters of tabulate and encrusting *Acropora*-dominated wall line beyond A1. Although the rocky wall is steep, its surface was also quite complex with ledges, large crevices, and overhangs built from dead corals and colonized by gorgonians, soft corals, and crinoids. Spur and groove structures are observed in the shallowest reef terrace of Apo Reef extending up to a depth of 18 m at the base of A2. A2 is dominated by branching and tabulate **Fig. 2 A** Relief chart of the bathymetry around Apo Reef, Occidental Mindoro based from multibeam echosounder surveys. White boxes indicate the extent of three-dimensional renders from (B)–(D). Points indicate locations where the ROV is deployed. Three-dimensional renders of the bathymetric features in Apo Reef in **B** North Atoll, **C** within the depression between the North Atoll and South Atoll, **D** Apo Island, and **E** South Atoll. Reef terraces with their outer edges are outlined by white dashed lines; reef ridges are outlined by black dashed lines. Vertical exaggeration at \times 1.5

Acropora, with a few encrusting corals. Clusters of small and large sea fans, hydroids, and diverse sponges were seen interspersed with encrusting and a few plating corals such as *Mycedium*.

The wall from 58 m depth and deeper is covered in sand and rubble until the slope is interrupted by the terrace at A4, 74 ± 6 m. The terrace at A4 and its scree-buttress slope have patches of rocks that extend down to the lower mesophotic depths. Hydroids, sponges, soft corals, sea fans, and other gorgonians were found on top of dead corals at this depth. The wall beyond A5, 102 ± 7 m, had no lifeforms except crinoids (at 143 m) up to 149 m, and the maximum depth reached by the ROV. It should be noted that A3 terrace, present from the rest of the reef, is absent in Apo Island and may have been poorly formed within its slopes.

Apo Reef North Atoll

Eight terraces were mapped around ARNA. The northwest wall and the more protected areas of the reef area are wider as compared to its west wall. Terraces at the northwest wall are 47% wider than the rest of ARNA.

The shallowest sets of surveyed terraces occur at A1, 6.5 ± 0.5 , and A2, 20.5 ± 0.5 . The reef terraces at A1 and A2 are dominated by tabulate *Acropora* (Fig. [6](#page-8-0)). Beyond **Fig. 3** Surface features around Apo Reef include: Apo Island (**A**) is a sand shoal that has grown around rock outcrops similar to (**B**) Apo Menor Island. Surface features in Tubbataha Reef are sand shoals like the Ranger Station (**C**) and small protruding rocks (**D**) around Bird Islet

Fig. 4 A Bathymetry, **B** slope, and **C** curvature map of the seafoor around Apo Reef

Table 2 Summary of the depth ranges of terraces around Apo Reef, Occidental Mindoro, and Tubbataha Reef, Palawan derived from collected bathymetric data

Measured terrace depth $(RTd) \pm \sigma RTd$ (m)						
	Apo Island Apo Reef	North Atoll	Apo Reef South Atoll		Tubbataha Reef	
A1	7 ± 1	$6.5 + 0.5$	$9 + 5$	T1	$7 + 1$	
A2	14.5 ± 3.5	20.5 ± 0.5	$26 + 4$	T2	$19 + 5$	
A ₃		$62 + 2$	$48 + 3$	T3	70.5 ± 4.5	
A4	$74 + 6$	$76 + 2$	$76 + 4$	T ₄	$92 + 4$	
A5	$102 + 7$	$92 \pm 1, 106.$ $5 + 3.5$	$103 + 8$	T5	$116 + 6$	
A6		$151 + 5$	$137 + 2$	T6	$134 + 2$	
A7		$189 + 5$				

A2, the steep upper drop-off or wall has a diverse assemblage of tabulate and branching *Acropora*, as well as *Seriatopora*, *Millepora*, fat sponges, gorgonians, and encrusting *Porites*, among others. From the drop-off to a reef wall from A2, there is a decreasing cover of branching corals and an increasing cover of sea fans, other gorgonians, hydroids, fat sponges, vase sponges, barrel sponges, and encrusting corals. At depth, the terraces occur between A3, 62 ± 2 m; A4, 76 ± 2 m; A5a, 92 ± 1 m; A5b, 106. 5 ± 3.5 5 ± 3.5 m; A6, 151 ± 5 m; and A7: 189 ± 5 m (Fig. 5). Within A3 terrace, the seabed is covered by sand, rubbles, and dead corals, which are colonized by gorgonians. At 78 m, within A4, the maximum depth reached by the ROV, is a large sandy and rubbly area with few patches of gorgonians.

Fig. 5 Stacked profles generated from the bathymetric data across each area in Apo Reef (**A**) and hypsometric curve showing the distribution of depths in Apo Reef (**B**). **D** Stacked profles generated from the bathymetric data from Tubbataha Reef along with **E** hypsometric

curve of the data. The vertical extent of the gray bars indicated the depth range of each terrace. These ranges are compared to the reconstructed paleo sea levels in the West Pacifc region (**C**)

Apo Reef South Atoll

Six terraces were mapped around ARSA. The west side has distinct sub-vertical slopes between 30 and 72 m. In contrast, ARSA has gentle slopes toward its southeastern margin. Terraces found facing southeast are 17% wider than the rest of the reef.

The shallowest terrace in South Atoll is A1 at $9+5$ m. The reef within A1 is mostly composed of tabulate *Acropora*, branching corals, and massive *Porites* (Fig. [6](#page-8-0)). The forereef slope starting beyond A1 has among the most diverse, extensive, and contiguous live coral coverage seen in Apo Reef. A1 terrace then gradually transitions to a deeper terrace A2 at 26 ± 4 m. Approaching A2 terrace, tabulate and branching *Acropora*, other branching corals, and foliose corals are interspersed with soft corals, but foliose corals of *Montipora* start to dominate. The steep slope area beyond A2 has foliose corals along with a few hydroids and gorgonians. The reef then drops into a steep wall which is broken by the terrace at A3, 48 ± 3 m. A3 terrace contains plating and encrusting corals, including *Porites*, and dead corals colonized by large sea fans, whip corals, and crinoids. Beyond A3, the rocky wall was colonized by large sea fans and gorgonians. The wall beyond A3 toward A4, 76 ± 4 m, is covered mostly by sand and rubbles, with some relatively fat, rocky patches colonized by sea fans, whip corals, and crinoids. Smaller terraces were also identifed at A5, 103 ± 8 m, and A6, 137 ± 2 m, within the reef wall (Fig. [5\)](#page-7-0).

An east–west-oriented depression ranging from 20 to 49 m deep separates the ARNA and ARSA (Fig. [2C](#page-5-0)). This depression is deeper toward the West. Several discrete reef mounds with heights of 2 to 15 m are scattered within this area. Ridges occur within the west side of this depression and in the southwest portion of the atoll. These ridges rise about 10 m from the seafoor from the edge of terraces that are shallower than 30 m. The tops of the ridges are bimodal with peaks at depths of 14 m and 28 m. At least five sets of ridges are found to run subparallel to each other (Fig. [2](#page-5-0)C).

Tubbataha Reef North Atoll

Tubbataha Reef North Atoll (TRNA) rises from depths of 500 m and is elongated NE-SW following the trend of the Cagayan Ridge. The shape is typical of an atoll with a shallow reef crest which rises close to the surface and a 40-m-deep lagoon (Dygico et al. [2013\)](#page-14-26). Shallow sand bars are found in the northeast and southern regions of the reef, on Bird Islet and Ranger Station respectively (Figs. [7](#page-9-0) and [8](#page-10-0)).

Terrace morphology observed on TRNA

Five terraces were identifed from the bathymetric data of TRNA. The shallowest mapped terrace of TRNA, T1, is at 7 ± 1 m (Fig. [5\)](#page-7-0). Terraces in the eastern section are wider by 26% compared to the west. ROV coverages in TRNA show that branching *Acropora* are dominant in the upper 8 m (Fig. [9\)](#page-11-0). *Porites*, *Millepora*, *Heliopora*, *Favites*, *Goniopora*, and *Leptoria* are also identifed within T1. The shallow area is interspersed with sandy regions containing coral rubbles.

The expansive shallow T1 terrace then breaks to the deeper T2 terrace at 19±5 m. Tabulate *Acropora* and plating *Porites rus* are predominant within T2. Other identifed corals are plating forms of *Montipora*, *Echinophyllia*, and *Pachyseris*. Coral heads of *Fungia*, *Lobophyllia*,

Fig. 6 Photographs from the ROV deployment show the composition of the seabed at diferent depths in Apo Reef. **A** Shallowest terrace within A1 at 8 m dominated by branching *Acropora*; **B** reef wall at 12 m covered by scleractinian corals *Acropora* and *Porites*; **C** terrace within A2 at 30 m dominated by foliose *Montipora*; **D** reef wall at 36 m containing encrusting corals, hydroids, and sponges; **E** terrace

at A4 at 73 m covered mostly by sand and rubbles with few mesophotic communities of sea fans and hydroids; and **F** terrace at A5 93 m, covered mostly by sand and rubbles with few sea fans. **G** Schematic cross-section of the depth profle in Apo Reef and the dominant composition of coral genera and seabed material per depth based on ROV observations

and *Symphillia* were also identifed. Beyond T2, the slope becomes sub-vertical. This also marks the base of spur and groove structures within the reef. Hard corals only occur within a reef wall until 36 m. These include *Diploastrea*, *Porites*, *Pachyseris*, *Oxypora*, and *Leptoseris*. Beyond 36 m, sea fans, soft corals, and sponges are usually seen along the reef slope and terminations of the terraces.

The steep slope of the reef wall is broken by smaller terraces T3 at 70.5 ± 4.5 m, T4 at 92 ± 4 , T5 at 116 ± 6 m, and T6 at 134 ± 2 m. Terraces T3 to T6 are not as defined as T1 and T2 due to the steepness of the slope (Fig. [8\)](#page-10-0). Reef walls are of bare carbonate rock, while coral rubbles and sand dominate the gentler regions of the seafoor. Few sea fans and sponges are identifed in these depths. ROV observations reached a maximum depth of 156 m on a barren rocky slope within the east side of the reef.

Discussion

Formation and sea‑level history

The rise of sea level since the LGM with intervening episodes of relative stillstand is considered the main driver for the staircase-like morphology of the reef terraces in Apo Reef and TRNA. A pair of terraces and scarp is interpreted as the former coral reef flat and reef front, respectively. The series of terraces were formed through subsequent backstepping during rapid rises of sea level and eventual re-establishment and progradation in a higher position during stillstands. The terraces then are taken as having formed during a relative sea-level stability while the scarp height approximates the magnitude of sea-level change.

Fig. 7 Three-dimensional renders of the bathymetry in Tubbataha Reef on the west section (**A**) and east section (**B**) show reef terraces with their outer edges outlined by white dashed lines. **C** Location of

Highly variable vertical accretion rates were observed in the Indo-Pacifc region from 1 to 30 m/ky and averaging at 6–7 m/ky in framework-dominated reefs (Montaggioni [2005\)](#page-16-1). Indo-Pacifc reefs develop with lower vertical accretion rates at an average of 4.4 m/ky compared to Caribbean reefs which grow at an average of 6 m/ky (Dullo [2005\)](#page-14-27). Within the Philippines, faster accretion rates were recorded in Currimao, Ilocos Norte at 10 to 13 m/ky (Shen et al. [2010](#page-16-8)). Due to this variability, reefs can easily keep up with small sea-level perturbations. Furthermore, the data of Shen et al. [\(2010\)](#page-16-8) and Janer et al. ([2023\)](#page-15-11) for the coral reefs in Currimao and Pag-asa Island, respectively, provide very fast rates of coral reef progradation. Borehole data in Currimao indicate progradation that can reach 75 m/ky (Shen et al. [2010](#page-16-8)). The morphology of reef terraces in Pag-asa Is. provides an estimate of the progradation rate that exceeds 150 m/ky (Janer et al. [2023\)](#page-15-11). The width of the terraces also provides indications of the duration of relative sea-level stability and the infuence of oceanographic factors that contributed to their development.

survey sites in Tubbataha Reef North Atoll. Yellow boxes represent areas surveyed by multibeam echosounder surveys. Points indicate locations where the ROV is deployed

Table [2](#page-6-2) summarizes the measured range of terrace depths at both sites. Within the last 19,000 years in the West Pacifc, the most widely recorded meltwater pulses include post-19 ka MWP, MWP-1a, and MWP-1b. Post-19 ka MWP is known as a rapid rise from 120 m following the Last Glacial Maximum (Clark and Mix [2002;](#page-14-28) Yokoyama et al. [2001\)](#page-17-5). Records from Bonaparte Gulf, Australia, indicate a 10–15 m rise in sea level from the LGM (Clark et al. [2004\)](#page-14-8). MWP-1a involves a 17.9 m jump in sea level from 14.65 ka (Brendryen et al. [2020;](#page-14-11) Lin et al. [2021;](#page-15-10) Weaver et al. [2003\)](#page-17-17). The depth of this jump in sea level ranges from 80 to 96 m (Hanebuth et al. [2000](#page-15-5), [2011\)](#page-15-26) and 80 to 95 m (Liu et al. [2004](#page-15-25)). The younger and shallower MWP-1b is an 8–11 m rise in sea level that occurred after 11.5 ka (Abdul et al. [2016;](#page-14-10) Bastos et al. [2022](#page-14-29); Blanchon et al. [2021](#page-14-30); Harrison et al. [2019](#page-15-8); Tian et al. [2020\)](#page-17-18). The extensive terraces at A6 to A3 in Apo Reef and T6 to T3 in TRNA (Fig. [5](#page-7-0)) are potential records of reef establishment around the events of 19 ka MWP, MWP-1a, and MWP-1b. In particular, terraces A3 and T3 are coeval with the records from the Sulu

Fig. 8 A Bathymetry, **B** slope, and **C** curvature map of the seafoor within the surveyed sections in Tubbataha Reef

Sea during the Younger Dryas preceding the sea-level rise during MWP-1b (Linsley and Thunell [1990\)](#page-15-27). During this period, oxygen isotope records indicate that the Sulu Sea experienced lower sea surface temperatures and lower salinity due to increased riverine discharge (Linsley and Thunell [1990\)](#page-15-27). Such conditions contribute to slower reef growth during the formation of terraces A3 and T3.

The terraces at A1 and T1 are interpreted to have formed within the 6–7 ka highstand observed at 0.3–1.5 m in Palawan Island by Maeda et al. ([2004\)](#page-16-5). Holocene records likely kept pace with vertical accretion after the mid-Holocene highstand. These comprise the shallowest reef in both sites and are also associated with the modern shallowest reefs in the region. Both Apo Reef and TRNA have no marine terraces higher than the present Holocene paleo sea levels. The emergent limestone outcrops in Apo Reef are well cemented and lithifed. These outcrops are unlike the observed emergent Holocene reefs in the Philippines which commonly are fssile and porous with visible bioclasts (Gong et al. [2017](#page-14-31); Shen et al. [2010\)](#page-16-8). There are also no tidal notches above present sea levels around these limestone outcrops. In TRNA, the only emergent features are sandy shoals and coral boulders. The absence of indicators of higher than present Holocene paleo sea levels suggests that Apo Reef and TRNA are undergoing subsidence and are consistent with their atoll morphologies. This subsidence also allowed for vertical space for accommodating the growth of the shallowest modern reefs.

Alternatively, former coral reef deposits may have undergone marine terrace formation during relative stillstands forming a terrace on the seaward side and a scarp on the landward side (Kershaw and Guo [2001\)](#page-15-4). The terraces and scarps can also be inherited topography from the existing carbonate platform that was formed pre-LGM. However, a post-LGM origin is favored because of the well-developed extant reefs which indicate rapid coral growth in the two study sites. Reef development from MIS 5e to MIS 2 is expected to occur in an irregular manner due to the general pattern of declining sea levels interrupted by brief but temporary rises in sea level (Waelbroeck et al. [2002\)](#page-17-19). It is expected that with the sub-aerial exposure of much older terraces, they would be discontinuous. The traced terraces, though, show continuity throughout the reefs. Short-lived transgressions, coupled with wave erosion during subsequent sea-level declines, result in minimal to no suitable surfaces for the establishment of future reef growth (Pastier et al. [2019](#page-16-26)).

The depth approximation in this study should be noted as simplistic. Discerning the precise timing for the formation of the terraces based solely on reef morphology has inherent uncertainties. Using geomorphic indicators for sea level is dependent on the tidal range of the sites (Horton et al. [2018\)](#page-15-28). Attenuating growth of coral reefs with depth also poses compounding uncertainties, with the uppermost terraces T1 and A1 likely accreting at the present time. The terraces are also subject to bioconstruction and deposition of rubble material closer to the toes of slopes. With these in mind, these interpretations should be viewed from a larger perspective with meter-scale approximations for the described events. Control on the timing of growth of the terraces should be considered for future studies by collecting samples through the reef.

Factors afecting reef growth

Antecedent topography is a primary determinant for growth patterns of modern reefs (Dechnik et al., [2015](#page-14-32), Salas-Saavedra et al. [2018\)](#page-16-27). Steep slopes inhibit progradation and result in more discreet reef features (Grigg et al. [2002](#page-15-3); Woodroffe and Webster [2014](#page-17-3)). The presence of small, outcropping karstic rocks on Apo Reef provides evidence for an antecedent foundation for modern reef growth. These outcrops are related to the offshore platform carbonates of Nido Limestone which are mapped extensively north of Palawan and have the shallowest seismic records in the area of Apo Reef (Franke et al. [2014](#page-14-24); Steuer et al. [2013](#page-17-13)). The base of Nido Limestone is dated Late Oligocene to Early Miocene and is coeval with the onshore units of St. Paul Limestone (Saldivar-Sali et al. [1981;](#page-16-28) Steuer et al. [2013\)](#page-17-13). Antecedent topography also explains its irregular shape and separation of reef components and the relatively gentle slopes around

Fig. 9 Photographs from the ROV deployment show the composition of the seabed at diferent depths in TRNA. **A** Shallowest terrace within T1 at 5 m dominated by branching *Acropora* and *Porites*; **B** edge of the T2 terrace at 18 m with identifed plating *Porites rus*; **C** terrace within T2 at 24 m covered by tabulate *Acropora*, and plating *Porites* and *Fungia*; **D** reef wall at 36 m containing encrusting *Lep-*

toseris, sea fans, hydroids, and sponges; **E** reef wall at 65 m containing bare rock and sand along with some sea fans and sponges; and **F** terrace T4 at 95 m is covered mostly by sand and rubbles with few sea fans. **G** Schematic cross-section of the depth profle in TRNA and the dominant composition of coral genera and seabed material per depth based on ROV observations

the southeastern area of the reef. Steep slopes and antecedent topography are the primary limitations for reef progradation in TRNA, and as a result, only the shallowest platform becomes extensive. Combined with unrestricted vertical reef build-up, this resulted in the steeper slopes around TRNA.

Wave energy surrounding a reef also determines the growth pattern of a reef platform. Reef growth is faster in windward reefs than in leeward reefs because exposure to wave energy optimizes mixing and nutrient uptake (Hongo & Kayanne [2009](#page-15-29)). However, stronger waves such as large oceanic swells and storm currents can cause high mortality and erosion of reef-building corals, therefore inhibiting reef growth (Grossman & Fletcher, [2004](#page-15-30)). The unique position of the Apo Reef in Mindoro Strait exposes it to dynamic nutrient-rich currents that move between the

South China Sea and the Sulu Sea, predominantly toward the southeast direction (Pullen et al. [2011](#page-16-21)). Apo Reef is in a more open location from incoming southwest monsoons. Owing to more energetic waters, spurs and grooves are observed on the southwest side of Apo Island. Most well-formed terraces in Apo Reef are located in the more protected areas of the reef, away from the southwest, experiencing optimal wave energies for building up reefs. Being located in the middle of the Sulu Sea, TRNA is openly exposed to energetic waves and currents (Pullen et al. [2011\)](#page-16-21). Dominant wind and wave patterns around TRNA are dictated by monsoons, with higher mean values coming from the southwest and northeast. This condition also contributes to the poor width of terraces in the surveyed areas.

Water clarity and temperature gradients of the oceans infuence the depth limits of coral growth. High sedimentation rates generally have adverse efects on coral reefs and are associated with lower growth rates and reef demise (Kennedy and Woodroffe [2002](#page-15-2); Perry et al. [2012](#page-16-29); Webster et al. [2018\)](#page-17-20). Oceanic reefs, like Apo and Tubbataha Reefs, are free from the efects of terrestrial sedimentation. The warm setting of the Sulu Sea and its surrounding waters also translate to warmer temperatures at depth (Gordon et al. [2011;](#page-15-31) Pullen et al. [2011](#page-16-21)). The depth limit of hard coral growth infuences the extent to which reefs can grow to catch up with sea-level rise (Webster et al. [2018](#page-17-20)). Both Apo Reef and Tubbataha Reef have recorded hard corals that cover up to depths of 51 and 36 m, respectively. The presence of hard corals in these depths is indicative of the resilience of the reef to changes in sea level.

Reef crests, once submerged, develop into reef ridges (Grigg et al. [2002;](#page-15-3) Woodroffe and Webster [2014](#page-17-3)). In Apo Reef, these reef ridges are common within the depression that separates the atolls as well as the inner part of ARSA. These ridges represent the position of the reef crest that has constructively caught up with sea level (Woodroffe [2008](#page-17-2)). Alternatively, these are also parallel progradational ridges formed by the successive accumulation of coarse material during extreme wave events (Kench et al. [2022](#page-15-32)). This explains its formation within more sheltered areas of the reef. The distribution of these ridges in two depths at 14 m and 28 m indicates two periods of sea-level stability during its formation. These reef ridges may also be erosional (Grigg et al. [2002\)](#page-15-3) but can only be confrmed if sampled or dated directly.

Departures from eustasy

The departure of the terrace depths from expected sea levels in the West Pacifc considers two factors: glacioisostatic adjustment (GIA) and tectonic motion. The study sites are located in a far-feld region at the equator. GIA effects in the region account for a change of about−0.3 mm/year in the study area (Milne and Mitrovica [2008\)](#page-16-30). This accounts for records of Holocene highstand at 2–3 m around Southeast Asia (Mann et al. [2019;](#page-16-31) Meltzner et al. [2017](#page-16-32)) during the past 6.5 ka BP (Li et al. [2023\)](#page-15-33). Maeda et al. [\(2004\)](#page-16-5) documented Holocene highstand tidal notches at 0.3–1.5 m above mean sea level in the central part of Palawan formed during around 6 ka BP. There are also records of undated emergent tidal notches found at 0.4–2.0 m above mean sea level along the coastlines of Sablayan and Sta. Teresa in Mindoro Island (Maeda and Siringan [2004\)](#page-16-11). Existing nearby records indicate emergence, in contrast with the submergence in Apo Reef and Tubbataha Reef. This also implies that vertical motions in Apo Reef and Tubbataha Reef are separate from those of the nearby Palawan and Mindoro Islands. Considering the extent of GIA infuence and the compounding efect of subsidence, LGM is expected to occur below recorded levels in the West Pacifc at 120 m (Clark and Tarasov [2014;](#page-14-4) Peltier [2002](#page-16-4)).

Apo Reef has a complex setting as it is located near the subduction zone of Manila Trench (Aurelio [2000\)](#page-14-19). Two zones in this setting cause vertical changes: a zone of fexure experiences an overall uplift and a downbowing zone experiences subsidence (Fig. [10](#page-13-0), Dickinson [2001](#page-14-2)). The limestones exposed in Apo Reef represent older carbonate platforms (Steuer et al. [2013\)](#page-17-13), exposed during an earlier phase when Apo Reef reached the forebulge portion of the subducting slab. Apo Reef is only about 15 km from Manila Trench. This distance to the trench indicates that Apo Reef is now infuenced by subsidence due to the downbowing of the subducting slab (Dickinson [2013\)](#page-14-33). The subsidence of the crust is driven by discrete tectonic structures driven into the Manila Trench as it subducts under Mindoro Island (Rangin et al. [1988](#page-16-16)). The mismatch between the depth ranges of terraces between the three reefs in Apo Reef indicates varying magnitudes of vertical movement. The magnitude of subsidence in Apo Reef is estimated in two ways. On the shallowest mapped terrace, A1 at 9 m is the reef fat that formed during the 6.5 ka BP Holocene highstand. Using the depth diference from known records in this period, Apo Reef would have subsided by 10 m at a rate of 1.5 mm/year. This assumes that there is no accretion on the terrace after its formation. Alternatively, A6 terrace at 137 m corresponds to the terrace formed during the LGM which ended 19 ka. Given its depth diference with records of LGM levels, Apo Reef would have subsided by 17 m which would yield a rate of 0.9 mm/year. It is likely that subsidence in Apo Reef was not uniform or continuous through time given its location close to active tectonic structures (Chen et al. [2015](#page-14-34); Rangin et al. [1988](#page-16-16)). Subsidence rates ranging between 0.9 and 1.5 mm/year are proposed for Apo Reef.

Tubbataha Reef sits atop an extinct volcanic arc that ceased volcanism during the Miocene (Fig. [10,](#page-13-0) Rangin and Silver [1991](#page-16-20)). The morphology of Tubbataha Reef is characteristic of a classic Darwinian atoll where the reef sits on a volcanic substrate. Vertical movement in this setting is caused by the thermal cooling of the lithosphere. The observed terraces are the latest formation in the continuing reef accretion on the extinct island arc of Cagayan Ridge. The shallowest terrace T1 at 6 m depth is formed during the 6.5 ka BP highstand. Given this diference with known records in this period, Tubbataha Reef would have undergone 7 m of subsidence or about 1 mm/year subsidence during 6.5 ka BP. Alternatively, the LGM depth of T6 at 134 m indicates that Tubbataha Reef, in the past 19 ka, would have subsided by 14 m or by 0.7 mm/year.

Fig. 10 Schematic diagram illustrating diferent tectonic infuences on reef formation at the study sites: (**A**) old platform reefs located on the trench forebulge distal from Manila Trench (**B**) subsided as it moves closer to the trench. This served as the antecedent platform for the formation of Apo Reef. (**C**) Tubbataha Reef is formed by successive reef build-up atop the subsiding Cagayan Ridge

Subsidence rates ranging between 0.7 and 1 mm/year are proposed for Tubbataha Reef. Compared to Apo Reef, vertical movements due to thermal cooling are likely to be more gradual than episodic. These rates represent the difference in subsidence between an actively subsiding region versus a passively subsiding Cagayan Ridge.

Conclusions

The geomorphology of the seafoor around coral reefs reveals the history of sea-level change in a region. The bathymetry around Apo Reef, Mindoro, and Tubbataha Reef North Atoll, Palawan in the Philippines documents the occurrence of submerged terraces that were formed post-LGM. The morphology follows the non-uniform sealevel rise during the last deglaciation, characterized by meltwater pulses and stillstands, resulting in a staircaselike formation of terraces. The sites reveal relative submergence when compared to known records of sea-level change within the West Pacifc and the Philippines. Apo Reef experiences tectonic subsidence due to a downbowing lithosphere. Tubbataha Reef experiences thermal subsidence which is attributed to the continuing cooling of an extinct island arc.

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Author contribution J.M. conducted feld surveys, processed and interpreted the data, and led the writing and development of the paper. He is the primary author and worked with the coauthors on the Philippine government-funded projects, "Acquisition of Detailed Bathymetry for Coastal Erosion and Management," and "Geophysical Coral Mapping Project" which brought forth the fndings contained in this submission. All authors reviewed the manuscript.

M. A. helped in the development of the paper and provided important discussions on tectonics.

E. T. and M.D. conducted feld surveys, assisted in the processing of raw data, and helped organize the fnalized datasets used in the study.

E. D. conducted coral reef surveys and interpreted the coral composition data.

F.D. conceptualized the research work, assisted in several feld surveys, identifed appropriate methods, and provided overall guidance in the development of this paper.

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Data Availability The datasets generated in the study are available from the corresponding author on reasonable request.

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Declarations

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