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Quaternary coral, coralline algal and vermetid assemblages as sea-level indicators: a review
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Abstract:	Corals, coralline algae and vermetid gastropods are indirect (marine limiting) relative sea level (RSL) indicators. The precision in sea-level reconstruction based on fossils of those organisms depends on the likely paleodepth in which they grew. Constraining such paleodepth, depends in turn on the available information on the habitats of living counterparts. Diverse genera, species and species assemblages of corals, coralline algae and vermetids have historically been proposed as reliable indicators of narrow shallow depth ranges. However, the increased information on depth distribution of marine benthos in the last two decades has challenged some early assumptions about depth ranges of taxa considered diagnostic of precise paleodepths. Here, we test the reliability of coral, coralline algal and vermetid assemblages that have been extensively used in sea-level reconstructions in the light of data from Ocean Biogeographical Information System (OBIS) and other recently published data. In the Indo-Pacific province, these data support the use of the robust-branching and the shallow, high-energy encrusting coral assemblages with a 0-10-m uncertainty. In both cases many component species have unimodal distributions, and median and average water depths are shallower than 10 m. The reliability of these coral assemblages as indicative of shallow water depths is strengthened when corals are encrusted by thick plants of the coralline alga Porolithon gr. onkodes . According to OBIS data coralline algae of this species group in the Indo-Pacific are restricted to very shallow waters (97.5% probability of occurrence shallower than 0.6 m). However, such a narrow depth range, and the overall scarce data on coralline algal species in the OBIS database are questionable due to difficulties of coralline algal species identification with naked eye. A comprehensive survey of the modern distribution of coralline algal at One Tree reef (Great Barrier Reef) indicates that P . gr. onkodes has a log-normal distribution with median depth of less than 5 m and 97.5% of occurrence probability of thick crusts (> 0.2 mm) shallower than 10.5 m. Data on modern distribution of vermetids are scarce. In the OBIS database, vermetid species are reported from relatively wide depth ranges. However, relatively high densities (> 10 individuals/m ^{2}) on coral and coralline algal surfaces only occur from above mean low tide to some 6 m depth. In the Western Atlantic-Caribbean province Acropora palmata is the most precise RSL marker and no additional components of fossil assemblages improve its paleodepth information. The confident use of coralgal and vermetid assemblages as RSL indicators relies on the identification of fossil corals and coralline algae at the species or species-group level. The scarcity of available data highlights the need for further studies on distribution of coralline algal species and vermetid in modern coral reefs.

Quaternary coral, coralline algal and vermetid assemblages as sea-level indicators: a review

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ABSTRACT

Corals, coralline algae and vermetid gastropods are indirect (marine limiting) relative sea level (RSL) indicators. The precision in sea-level reconstruction based on fossils of those organisms depends on the likely paleodepth in which they grew. Constraining such paleodepth, depends in turn on the available information on the habitats of their living counterparts. Diverse genera, species and species assemblages of corals, coralline algae and vermetid gastropods have historically been proposed as reliable indicators of narrow shallow depth ranges. However, the increased information on depth distribution of marine benthos in the last two decades has challenged some early assumptions about depth ranges of taxa considered diagnostic of precise paleodepths. Here, we test the reliability of coral, coralline algal and vermetid assemblages that have been extensively used in RSL reconstructions in the light of data from Ocean Biogeographical Information System (OBIS) and other recently published data. In the Indo-Pacific province, these data support the use of the robust-branching and the shallow, high-energy encrusting coral assemblages with a 0-10-m uncertainty. In both cases many component species have unimodal distributions, and median and average water depths are shallower than 10 m. The reliability of these coral assemblages as

indicative of shallow water depths is strengthened when corals are encrusted by thick plants of the coralline alga *Porolithon* gr. *onkodes*. According to OBIS data, coralline algae of this species group in the Indo-Pacific are restricted to very shallow waters (95 % probability of occurrence shallower than 0.2 m and 99.6 % of records shallower than 6 m). However, such a narrow depth range, and the overall scarce data on coralline algal species in the OBIS database are questionable due to difficulties of coralline algal species identification with naked eye. A comprehensive survey of the modern distribution of coralline algae at One Tree Reef (southern Great Barrier Reef) indicates that *P*. gr. *onkodes* has a log-normal distribution with median depth of less than 5 m and 95 % of occurrence probability of thick crusts (> 0.2 mm) shallower than 8.8 m. Data on modern distribution of vermetids are scarce. In the OBIS database, vermetid species are reported from relatively wide depth ranges. However, relatively high densities (> 10 individuals/m^2) on coral and coralline algal surfaces only occur from above mean low tide to some 6 m depth. In the Western Atlantic-Caribbean province *Acropora palmata* is the most precise RSL marker and no additional components of fossil assemblages improve its paleodepth information. The confident use of coralgal and vermetid assemblages as RSL indicators relies on the identification of fossil corals and coralline algae at the species or species-group level. The scarcity of available data highlights the need for further studies on distribution of coralline algal species and vermetid in modern coral reefs from a variety of oceans and reef settings.

INTRODUCTION

In the last two decades, an extraordinary research effort has focused on Quaternary sea-level variations, from local relative sea level (RSL) at particular time intervals to eustatic sea-level (ESL) changes throughout time and their relationships to Earth climate. The elaboration of schemes to categorize past RSL indicators have been applied to thousands of sites worldwide. This has led to the accurate definitions of the type and precision of potential RSL markers and to the development of standardized

protocols for paleo-RSL reconstructions (Rovere *et al.*, 2016). According to those protocols, several landforms can be used as precise indicators of past RSL position (Rovere *et al.*, 2016), while only a few fossil biogenic structures, such as vermetid trottoirs, can be considered accurate markers of ancient RSL (Laborel, 1986).

Marine fossils in growth position, or *in situ*, evidence a marine or lower limit (marine limiting) for the RSL uncertainty (Rovere *et al.*, 2016), but the amount of uncertainty (i.e. vertical error) depends on the likely depth position of the fossil at the time of its growth. Consequently, fossils of organisms that live in narrow depth ranges would be the most appropriate to estimate RSL at the time they grew. Obviously, the use of particular taxa, from high-order groups to species, for RSL reconstruction depends on the knowledge about their modern habitat depth ranges, which has been improving with increasing data on distribution of marine species.

Some groups of zooxanthellate corals have traditionally been considered key fossils for RSL reconstructions due to the presumed shallow habitats with narrow depth ranges of their living species (Lighty *et al.*, 1982; Davies & Montaggioni, 1985; Fairbanks, 1989; Cabioch *et al.*, 1999; Montaggioni, 2005; Montaggioni & Braithwaite, 2009; Woodroffe & Webster, 2014; Camoin & Webster, 2015). They also have a high potential for precise, radiometric dating using U-series and radiocarbon, and a worldwide distribution in the tropical/subtropical regions, in which many areas are far-field with glacio-isostatic adjustment (GIA) minimised (Hibbert *et al.*, 2016).

Corals may play a secondary role as RSL indicators in uplifting areas or in stable regions for records of ESL higher than present-day, such as the Last Interglacial (MIS5e). In both cases, precise geomorphic RSL indicators, including coral-reef terraces are usually available (Rovere *et al.*, 2016). In such instances, the dating potential of corals would be more relevant than their paleodepth meaning. However, in subsiding areas and for periods of ESL lower than present-day, landforms can be less conclusive or even absent, and RSL reconstruction needs to be based on data

sedimentological and paleontological data from drill cores or collected from the sea floor via ROV, submersible or dredging.

In these cases, individual coral genera and species, and coral assemblages have been used to estimate paleodepth of fossil reef deposits and to subsequently reconstruct RSL changes (e.g. Fairbanks, 1989; Bard et al., 1996; Deschamps et al., 2012; Yokoyama et al., 2018). In Quaternary reefs, paleodepth has been estimated based on the known depth distributions of living members of the same coral taxon or assemblage. This approach has been applied using single species, such as *Acropora palmata* in the Caribbean reefs (e. g. Lighty *et al.*, 1982; Fairbanks, 1989 Bard *et al.*, 2016; Mortlock *et al.*, 2016) or assemblages defined by a combination of component species and their morphology (e. g. Nakamori, 1986; Pirazzoli & Montaggioni, 1988; Bard et al., 1996; Yokoyama et al., 2018). Logically, the depth ranges of the involved taxa have historically been estimated according to the ecological information, in some cases limited, available at that time.

As stated by Hibbert *et al.* (2016), in the last two decades the increasing use of autonomous underwater vehicles (AUV), and improvements in diving technology (rebreathers, mixed air gases) have extended the depth range of surveys on the distribution of corals species. Many of these surveys cover mesophotic reefs, which mainly occur at depth ranges of 30 to 40 m but can extend down to 150 m (Hinderstein *et al.*, 2010), and have been the subject of intense research in the last years. This new ecological information is partly published in a number of papers (for example Muir *et al.*, 2015), although most of the available data come from the Ocean Biogeographical Information System (OBIS, https://obis.org) and IUCN (International Union for Conservation of Nature; https://www.iucnredlist.org). The available information on coral ecology and biogeography shows that occurrence and reliability of coral RSL indicators vary geographically between localities within oceans, and between oceans. Even within localities, coral depth ranges might change depending on geomorphology, energy and sediment input (Done, 1982; Braithwaite, 2016). On the other hand, this knowledge on

the environmental distribution of reef builders, including their depth ranges, is crucial to reconstruct the response of reef ecosystems to spatio-temporal variations in global to local environmental parameters, such as climate, sea level, water quality, turbidity in the past (Blanchon *et al.*, 2009; Camoin *et al.*, 2012; Woodroffe & Webster, 2014; Camoin & Webster, 2015; Toth *et al.*, 2015; Webster *et al.*, 2018).

The accuracy and usefulness of coral RSL indicators can be improved by adding depth-related information about co-existing coralline algae (CAA) and vermetid gastropods. Paleodepth interpretations based on CAA and vermetids, which are common encrusters contributing to reef growth, have been used to reconstruct RSL from fossil reefs (Davies & Montaggioni, 1985; Pirazzoli & Montaggioni, 1988; Bard *et al.*, 1996; Camoin *et al.*, 2001; Cabioch *et al.*, 2003; Abbey *et al.*, 2011; Deschamps *et al.*, 2012; Dechnik *et al.*, 2015, 2017; Gischler *et al.*, 2016, 2018b; Webster *et al.*, 2018; Yokoyama *et al.*, 2018; Humblet *et al.*, 2019). The living and fossil representatives of these two groups have received less attention than corals, and the available literature on the depth ranges of the reef-related species is relatively scarce and concentrated in a few geographic areas (Adey, 1986; Dechnik *et al.*, 2017; Humblet *et al.*, 2019 and references there). The OBIS database includes a number of tropical/subtropical species of both groups but in many cases the records are too few to be of statistical significance. As shown below, despite these limitations, CCA and vermetid gastropods show potential to improve the accuracy of RSL reconstruction based on coral indicators.

The reliability of coralgal assemblages (coral and CCA) and vermetids in reef deposits as RSL indicators also depends on the feasibility of distinguishing *in situ* framework from allochthonous rubble. In the latter case it is crucial to understand the paleoenvironmental setting in which the rubble accumulated. Protocols or suites of criteria have been proposed to reduce uncertainties regarding the autochthony of reef components since the early works on corals as paleo-RSL indicators (Lighty *et al.*,

1982; Montaggioni *et al.*, 1997; Montaggioni & Faure, 1997; Camoin *et al.*, 2001; Webster & Davies, 2003; Blanchon & Perry, 2004).

Based on worldwide records of living corals included in OBIS, Hibbert *et al.* (2016) suggest that corals are "depth-generalists", with restricted depth ranges only when individual species are considered. Consequently, they suggest that fossil corals should be identified at the species level to reduce uncertainty in RSL reconstructions. Using OBIS and IUCN databases Hibbert *et al.* (2016, 2018) assessed modern depth distribution of coral species previously used in RSL reconstructions, questioning blanket assumptions of coral paleodepth interpretations and providing depth-range parameters, such as median depth, maximum depth, and probability distribution with confidence intervals for individual coral taxa.

Following a similar approach, in this paper we use publications on coral reef ecology, OBIS and IUCN databases to assess the reliability and precision of reef-builder assemblages as RSL markers. We explore the potential of the coralgal/vermetid assemblages to provide improved constraints and consistency in paleo-RSL reconstruction based on these important reef builders. This review is particularly focused on the CCA and vermetid components of the assemblages, which have not been comprehensively incorporated into previous assessments.

METHODS

A primary source of data and interpretations included in this review is the literature about depth distribution and potential use for RSL reconstruction of living coral, CCA and vermetid assemblages. Following a historical sequence, we focused on papers and monographs proposing biotic zonations of corals, CCA and vermetids in modern reefs. Within the information included in those works, we concentrated on assemblages of these organisms that were considered the best indicators of shallow depths and, consequently, the most precise markers of RSLs. We also refer to published reports on Quaternary reefs applying the occurrence of particular coral, coralline algal and

vermetid assemblages to reconstruct RSL. The examined works are listed in the Supplementary table, detailing location, age, reef habitat, depth/paleodepth, assemblage components, and source of information for paleodepth interpretation. The data included in the table consists of verbatim quotes from the primary papers.

We also used data in the Ocean Biogeographical Information System (OBIS, https://obis.org, October 2021) on depth distribution of genera and species of corals (in the Indo-Pacific province), CCA and vermetid gastropods that are reported in the literature as the most precise RSL indicators (Table 1). We used the R package robis version 2.3.11 (Provoost & Bosch, 2017) to download the occurrence data for the selected species of corals, coralline algae, and vermetids. The following parameters from the OBIS records were used to filter the data for analyses: basis of record, minimum and maximum depths of the record in meters, and occurrence remarks. We only used human observations (basis of record), with a difference between maximum and minimum depths of 1 meter for corals and 3 meters for CCA and vermetids, and used the occurrence remarks to find and remove duplicate records. We used a larger min/max depth range for observations on CCA and vermetids to increase the number of records available for the analyses. Duplicates were identified particularly for records associated with the National Institutes for Water and Atmospheric Research (NIWA), which refers to other OBIS datasets in most instances. Depth outliers were also excluded from the data analyses. A total of 54 species and 3 genera of corals, 6 species of CCA, and 2 species and 1 genus of vermetids were examined from OBIS. The number of filtered records per species ranged from 18 (*Acropora palmerae*) to 2954 (*Pocillopora damicornis*). We calculated the summary statistics and found the best-fitting distribution for each species using the R package fitdistrplus version 1.1-3 (Delignette-Muller & Dutang, 2015). All the depth data was increased by 0.01 to eliminate zero values and allow us to test more distributions. The normal, log-normal, logistic, exponential, Weibull, and gamma distributions were fitted and the distribution with the lowest Akaike information criterion (AIC) value was selected as the best-fit.

Since we are primarily interested in the deepest habitat for each species, we used a one-tailed approach and calculated the value of the 95 percentile ($p < 0.05$) from the chosen distribution (Tables 2 and 3). We also present the percentage of records shallower than 6 m, a depth traditionally considered the lower limit of high-energy shallow-water coral assemblages (Montaggioni & Braithwaite, 2009 and references therein). Of the coral species analysed, 23 were found to have bimodal distributions with a significant amount of deep-water (mesophotic) records. They fit poorly with all the distributions tested and are omitted from the results.

For CCA and vermetids we also present new data on the depth distribution of living taxa recorded at One Tree Reef in the southern Great Barrier Reef (GBR), which were partly reported in the supplementary material in Dechnik *et al.* (2017). In that study, CCA sampled from 0 to 30 m depth were identified in the lab with the help of optical microscopy and SEM, reducing the uncertainty of taxon identification common in field surveys. In addition, vermetid abundance was estimated in CCA crust sections as is usually observed at fossil reef outcrops and drill cores. Data from the IUCN Red List on depth limits of coral species characteristic of coral assemblages considered the best RSL indicators are included in Table 2 (International Union for Conservation of Nature Red List; https://www.iucnredlist. org).

Although most records in the OBIS database are updated to the most recent classification schemes, for corals we use the latest scheme defining the families Merulinidae, Montastraeidae, and Diploastraeidae (Huang *et al.*, 2014), Lobophylliidae (Huang *et al.*, 2016) and Mussidae in the Atlantic Ocean (Budd *et al.*, 2012). The classification of Veron (2000) is followed for other families. The updated taxonomy for CCA used here can be found in ALGAEBASE (https://www.algaebase.org) as well as in specific papers referred to in the CCA section. For vermetids we use the scheme in WORMS (2021, https://www.marinespecies.org) which includes the taxonomy proposed by Golding *et al.* (2014).

RESULTS

Coral assemblages

Western Atlantic/Caribbean

Modern

Acropora palmata has been widely used as the main, mostly single past RSL indicator (Table 1 and Supplementary table) since the work of Lighty *et al.* (1982), who proposed a depth range of < 1-5 m for frameworks of this species based on many previous observations of different authors across the Western Atlantic. The applicability of *A. palmata* as RSL indicator using modern depth distribution data of the species at regional to local scales has been largely detailed by Hibbert *et al.* (2016, 2018). A more precise RSL reconstruction can be attained when the *A. palmata* records are characterized with additional observations on facies and taphonomy. Colonies of *A. palmata* are considered indicative of reef crest/flat facies formed in less than 2 m depth when covered by thick crusts of CCA (Blanchon & Perry, 2004; Stathakopoulos *et al.*, 2020). In the Caribbean no assemblage/multispecies approach would improve the results that could be obtained by using *A. palmata* alone. A few papers (Ludwig *et al.*, 1996; Fruijtier *et al.*, 2000) suggested that the optimum growth depth of other corals, such as *Orbicella annularis* (as *Montastraea annularis*) and *Pseudodiploria strigosa* (as *Diploria strigosa*), and *Colpophyllia* sp. is restricted to shallow water and can be used as paleo-RSL indicator. However, other authors question any narrow depth distribution of Caribbean corals, other than *A. palmata,* to the point of considering all of them "deep-water corals" (Khan *et al.*, 2017). However, species of *Pseudodiploria* (formerly known as *Diploria clivosa* and *D. strigosa*), have unimodal distributions with median and average values above 10 m, according to the OBIS database.

Fossil

Mesolella (1967) observed in the Pleistocene reef terraces in Barbados a coral zonation similar to that described in modern Caribbean reefs. Accordingly, he interpreted that the top of the zone characterized by *Acropora palmata* with thick CCA crusts indicates the paleo-mean low tide level. Since then, many studies have used the occurrence of *A. palmata* to reconstruct RSL and infer ESL (for example Fairbanks, 1989; Blanchon *et al.*, 2009; Muhs *et al.*, 2011; Abdul *et al.*, 2016; Khan *et al.*, 2017; Stathakopoulos *et al.*, 2020) or to interpret paleowater depth of reef deposits (see Supplementary table).

Indo-Pacific province

Modern

Coral assemblages characterized by coral morphology and taxonomic composition, together with other encrusters are typical of distinct environments with a defined depth range and can be used for reconstructing paleo-RSL. Davies and Montaggioni (1985) reported the results of a discussion panel in the 5th International Coral Reef Congress in Tahiti that summarized the knowledge at that time on reef growth and sea-level change. Following unpublished data of Faure (1982), they suggested that common species of *Acropora*, such as *A. abrotonoides* (as *A. abrotonoides* and *A. danai*) and *A. robusta*), are indicative of waters shallower than 10 m. Davies and Montaggioni (1985) also proposed that detailed vertical zonations of coral assemblages, such as those published by Done (1982) could have regional applicability for RSL reconstructions. The robust-branching coral assemblage (community, facies) was proposed as particularly precise, typical of upper forereef to outer reef flat settings and paleodepths of less than 6 m (Montaggioni & Faure, 1997; Cabioch *et al.*, 1999; Montaggioni, 2005, Table 1). Components can change depending on the region although dominant taxa, namely *Acropora robusta-danai* group, *A. humilis* group, and *Pocillopora verrucosa* are common in all reported localities. Other coral assemblages, such as the tabular branching community, dominated by *Acropora hyacinthus, A. cytherea,* and *Montastrea*

or a domal *Porites* community were considered less precise indicators of deeper slope

environments, outer reef flats or windward settings in lagoons (Camoin *et al.*, 1997;

Montaggioni & Faure, 1997). This community/assemblage scheme was followed by

Cabioch *et al.* (1999) who defined reef-building assemblages that can be used as

reliable paleo-RSL markers throughout the Indo-Pacific region (Supplementary table).

These authors provided more detailed accounts of coral species belonging to each

assemblage and stressed that components and distribution of these assemblages can

vary according to local environmental conditions (e.g. irradiance, water energy)

(Supplementary table). Montaggioni (2005) in his analysis of coral assemblages in the

Indo-Pacific maintained the assemblages proposed by Montaggioni and Faure (1997)

and Cabioch *et al.* (1999), and added three more coral-dominated facies: arborescent-

coral, foliaceous-coral and encrusting-coral facies (Table 1). Montaggioni and

Braithwaite (2009) in their synthesis of Quaternary reefs follow the scheme of

Montaggioni (2005) to define coral zonation in the Indo-Pacific province. These authors

acknowledge that coral growth forms, reflecting environmental conditions, are more

diagnostic in terms of zonation than species composition due to the overlap of species

distributions referring to works by Braithwaite (1971); Rosen (1971, 1975), Pichon

(1978), and Riegl and Piller (2000). According to Montaggioni (2005) and Montaggioni

and Braithwaite (2009), the robust-branching-coral assemblage, characteristic of

windward reef margins represents the most precise paleo-RSL marker based on fossil

corals, indicating coral growth shallower than 6 m. The domal, the tabular–branching,

arborescent, and foliaceous coral assemblage can extend to depths of 15-20 m. The

encrusting coral assemblage is limited to the top 10 m in high-energy settings, although

components of this assemblage (e.g., *Pachyseris speciosa*, *Leptoseris*, *Echinophyllia*)

can be dominant on reef slopes deeper than 20 m. The distributions of assemblages

might vary independently of depth, due to other factors such as wave energy (Rosen,

1971) and, locally, water temperature and turbidity (Braithwaite, 2016). In any case, on

steeper slopes or more turbid inner-shelf reefs, the coral assemblages adapted to

lower irradiance may extend into shallower parts of the reef slope (Done, 1982; Montaggioni & Braithwaite, 2009).

Quantitative surveys were conducted at One Tree Reef, southern Great Barrier Reef, by Dechnik *et al.* (2017) to investigate the distribution of corals, CCA and vermetid gastropods between 0 and 30 m in two contrasting wave-energy settings (i.e., windward and leeward slopes). *Acropora* gr. *humilis*, *A. robusta* and encrusting *Isopora* are dominant from 0 to 6 m on the windward margin, and *A*. gr. *humilis* and columnar *Isopora* are dominant from 0 to 3 m on the leeward margin. *Pocillopora* is common in both settings. These results are consistent with descriptions of the shallowest reef margin assemblages elsewhere in the Indo-Pacific province. Coral assemblages defined by Dechnik *et al.* (2017) below 6 m are characterized by massive *Porites*, associated with tabular *Acropora* down to 20 m, and from 20 to 30 m with encrusting *Montipora* on the windward margin, and *Seriatopora* and *Lobophyllia* on the leeward margin.

The available data in OBIS on depth distributions of component species of the assemblages believed to have the narrowest and shallowest range, i.e. the robust-branching and the shallow, high-energy subtype of the encrusting coral assemblages of Montaggioni (2005), strongly supports their use as paleo-RSL markers (Table 2, Figs. 1, 2).

Regarding the robust-branching assemblage, taking into account the OBIS database, whilst a few typical species such as *Acropora robusta* and *Acropora abrotanoides, Pocillopora grandis* (= *P. eydouxi*), and *Goniastrea retiformis* have a polymodal or bimodal distributions with wide depth range (0-55 m), many other component species, such as *A. humilis, A. aspera, A. nasuta, A. hyacinthus, A. latistella, A. gemmifera,* and *A. palmerae, Isopora palifera, Pocillopora damicornis, Leptoria phrygia, Favites flexuosa*, and *Goniastrea favulus* have unimodal distributions, and median and average depths of records shallower than 10 m (Table 2, Fig. 1). We note, however, that the bimodal distribution of *Acropora robusta* is not supported by the

published literature. Muir and Pichon (2019) do not identify *A. robusta* as a mesophotic reef-building coral species, and Muir *et al.* (2015) describe this species as exclusively shallow in North-East Australia. However, morphologically similar species, i.e., *A. abrotanoides* and *A. intermedia* (Wallace, 1999), were reported from the upper mesophotic zone in the Tuamotu Islands (Muir & Pichon, 2019) and American Samoa (Montgomery *et al.*, 2019), respectively.

Establishing precise probabilities of finding two or more of these species together in a defined depth range (for example the 0-6 m assumed in many papers as typical depth range for the assemblage) is difficult as the relative frequency of the species is highly variable and only provided in relatively few available data sets. However, the remarkable coincidence of mode, median and average depths of many component species suggest that the robust-branching coral assemblage when defined by several species is a reliable indicator of paleodepths shallower than 10 m (Fig.X; Table 2). In the case of *A. hyacinthus*, *A. latistella* and *G. favulus*, according to their probability distributions 95 % of the records would be shallower than about 10 m. In addition, as an average more than 80 % of the records of the assemblage components are shallower than 6 m (Table 2).

In the case of the high-energy subtype of encrusting coral assemblage (Montaggioni, 2005), according to OBIS data, some component species, such as *Montipora capitata*, *M. patula, Leptastraea purpurea*, and *Leptoseris mycetoceroides* have bimodal distributions and occur both in shallow and mesophotic reefs. However, the majority of species assigned to this assemblage (*Montipora monasteriata, M. danae, M. undata, Pachyseris speciosa, Echinophyllia aspera*, *Echinopora lamellosa, Cyphastrea microphthalma, C. serailia, Merulina ampliata,* and *Porites lutea*) mainly occur in shallow depths, with modes and medians well above 10 m and theoretical distributions with 95 % of records shallower than 10 m in a few cases (*A. microphthalma* and *P. lutea*) (Table 2, Fig. 2). As an average, 73 % of records of the components of this assemblage are shallower than 6 m.

Ideally, the depth distributions of the species should be based on local to regional surveys encompassing a wide depth range in the vicinity of the study site (Dutton *et al.*, 2015; Hibbert *et al.*, 2016; Dechnik *et al.*, 2017; Chutcharavan & Dutton, 2020).

Fossil

Nakamori (1986) assigned the Pleistocene coral assemblages in the Ryukyu Islands to a series of communities corresponding to living coral communities that are characteristic of different environments in fringing reefs in the archipelago. Nakamori (1986) considered two of those fossil communities (Community A, composed of branching *Acropora, Montipora,* and hemispherical *Porites,* and Community B, formed by tabular *Acropora*) indicative of reef crests developed almost at sea level. Following a similar approach, Pirazzoli and Montaggioni (1988) proposed that the co-occurrence of *A. abrotonoides* (as *Acropora danae = A. danai*) and *Acropora robusta,* together with distinct CCA and vermetids (see below) in the Holocene reef deposits from Tahiti corresponds to the modern "interlocking framework" at the reef margin in the island. Therefore, it would be characteristic of water depths shallower than 3 m. The coral-assemblage approach was systematized in several papers dealing with deglacial and Holocene deposits from the western Indian Ocean and Tahiti (Camoin *et al.*, 1997; Montaggioni *et al.*, 1997; Montaggioni & Faure, 1997, Supplementary table).

In the Ryukyu Islands, following the work of Nakamori (1986), paleo-RSL reconstructions for Pleistocene and Holocene reefs were based on observation of depth distributions of coral assemblages in living reefs fringing the islands (Iryu *et al.*, 1995; Nakamori *et al.*, 1995; Wallace, 1999) or direct observations on living reefs near the Quaternary reefs, suggesting high-precision (less than 2 m in some cases) RSL indicators (Webster *et al.*, 1998; Sagawa *et al.*, 2001; Kayanne *et al.*, 2002; Sugihara *et al.*, 2003; Hongo & Kayanne, 2009, 2011).

With slight variations in their paleodepth meaning, the coral assemblages proposed by Montaggioni and co-authors in the 90s and 2000s have been used as paleo-RSL indicators in reconstructions of reef development and RSL curves based on reef cores or samples collected from the sea floor in diverse localities across the Indo-Pacific. In particular the occurrence of the robust-branching coral assemblage has been considered indicative of paleodepths varying from 0-5 m to 0-10 m (Bard *et al.*, 1996, 2010; Galewsky *et al.*, 1996; Camoin *et al.*, 2001, 2004; Cabioch *et al.*, 2003; Webster & Davies, 2003; Webster *et al.*, 2004b, 2018; Frank *et al.*, 2006; Andersen *et al.*, 2008, 2010; Thomas *et al.*, 2009; Shen *et al.*, 2010; Abbey *et al.*, 2011; Deschamps *et al.*, 2012; Dechnik *et al.*, 2015, 2017; Gischler *et al.*, 2016, 2018a; b; Yokoyama *et al.*, 2018; Humblet *et al.*, 2019). In addition to the depth distribution proposed by Montaggioni's group, these papers refer to other works on Indo-Pacific coral ecology (see references in Supplementary table).

Coralline algae

Coralline algae are a group of red algae (Rhodophyta) that secrete calcium carbonate, high-Mg calcite, in their cell walls. They belong to four different, phylogenetically related orders (Corallinales, Hapalidiales, Sporolithales, and Corallinapetrales) in the class Floridophyceae (Jeong *et al.*, 2020). From an anatomical point of view, corallines can be geniculate (articulated) with uncalcified portions in their body, or non-geniculate, possessing a thallus (body) fully calcified except at the very surface. The non-geniculate or crustose coralline algae (CCA) are common in modern coral reefs (Fig. 3) and related habitats, encrusting hard substrates or as unattached nodules called rhodoliths. They are major builders (Adey *et al.*, 1982; Bosence, 1983, 1991; Littler & Littler, 1984) and contribute significantly to reef health and biodiversity, playing a role as settlement inducers of coral larvae (Morse *et al.*, 1996; Nelson, 2009; Vermeij *et al.*, 2011).

The first extensive synthesis of CCA as RSL indicators was presented by Adey (1986).

This author considered CCA assemblages as precise indicators of paleo-RSL in

tropical areas, with ± 2 m resolution near mean low sea level and increasing

uncertainty with increasing depth. This optimistic view is not fully supported by data on

CCA distribution gathered since then, but these data corroborate the potential of fossil

CCA to estimate past RSL.

Atlantic-Caribbean

Modern

Based on previous work of Adey (1975), Davies and Montaggioni (1985)

considered CCA (*Lithophyllum kaiseri* and *Porolithon antillarum*, as *Lithophyllum*

congestum and *Porolithon pachydermum*, respectively) reliable indicators of depths of

1-2 m. Adey (1986) described algal ridges as distinct features, consisting of massive

carbonate frameworks built largely by CCA with foundations on coral reefs or other

type of rocky substrate. Caribbean algal ridges extend from + 2 m above mean sea

level to – 6 m (Adey & Burke, 1976, 1977) but extensive framework develops only

close to or slightly above mean low sea level. These ridges are composed of

Lithophyllum kaiseri and *Porolithon antillarum* (as *Lithophyllum congestum* and

Porolithon pachydermum in Adey, 1986, respectively) and *Neogoniolithon*, with cryptic

species of *Paragoniolithon* (currently considered a synonym of *Neogoniolithon*) (Table

1)*, Hydrolithon, Sporolithon, Mesophyllum*, and *Lithothamnion* (Adey, 1986). According

to this author, on coral reefs in all oceans, thick (several cm scale) CCA encrustations

are typical of less than 6 m, whereas deeper CCA are thin and leafy. Regarding

taxonomic composition, assemblages dominated by *Porolithon* with cryptic *Hydrolithon*

and *Neogoniolithon* occur in less than 10 m. *Neogoniolithon* (including *Paragoniolithon*)

characterizes assemblages in depths from 10 to 30 m, and *Hydrolithon* dominates

assemblages deeper than 30 m (Adey, 1986). On the other hand, friable fringing

reefs/trottoirs of *Neogoniolithon strictum* are typical of very shallow water in protected

areas of Bahamas and Florida (Adey, 1986). A few years later, Martindale (1992) published a precise zonation of CCA in modern reefs in Barbados. Thick crusts of *Porolithon* sp. (*P. ?antillarum* as *P. ?pachydermum*) and *Lithophyllum* sp. (*L. ?kaiseri* as *L. ?congestum*) dominate in illuminated, shallow substrates (0-3 m). Thinner crusts of lithophylloids (as *Tenarea* sp.) predominate in slightly deeper water (3-8 m), and thin crusts of *Neogoniolithon* sp. and lithophylloids cover the well-lit surfaces between 8 and 16 m. Thin, foliaceous crusts of *Hydrolithon* sp., *Mesophyllum* sp., and *Lithothamnion* sp. characterize cryptic and deeper settings (20-50 m).

Following Geister (1977), Montaggioni and Braithwaite (2009) identify a CCA-dominated community, formed by 1–3 m thick crusts of CCA and sparse corals in the most exposed reef crests in the Western Altlantic-Caribbean province.

In the Abrolhos reefs in the eastern Brazilian shelf, Jesionek *et al.* (2016) and Amado-Filho *et al.* (2018), consider *Porolithon gr. onkodes* and *Melyvonnea erubescens* indicative of depths between 2 and 5 m (Table 1), whilst *Dawsoniolithon* gr. *conicum* (as *Pneophyllum conicum*) is found above 15 m.

One of the robust clades in the phylogram of the *P. onkodes* group proposed by Gabrielson *et al.* (2018) comprises the holotype of *Porolithon antillarum*, and the lectotype of *P. onkodes* f. *pachydermun* (i.e. the type of *P. pachydermum*, the ecological equivalent of the Indo-Pacific *P. onkodes* – see below - in the Caribbean, Adey 1986). The Atlantic *P. antillarum* and *P. pachydermum* were considered morphologically indistinguishable from, and younger synonyms of *P. onkodes* by Maneveldt and Keats (2014). Despite the morpho-anatomical similarity and traditional interpretations of ecological equivalence (Adey, 1979, 1986; Martindale, 1992), the depth distribution of *P. antillarum* (including *P. pachydermum* as a younger synonym) according to OBIS database is substantially different from the one of *P. onkodes* (Table 3, Fig. 4). While the latter is restricted to the upper few meters (see below), *P. antillarum* is reported in 31 records in a depth range from 3 to 80 m and average depths of 29 m ± 19.3 sd.

Fossil

In the Western Atlantic-Caribbean province, Mesolella (1967) considered thick crusts of CCA typical of the shallowest reef crest (mean low sea level) in the Pleistocene reef zonation in Barbados. Despite this early report, and the pioneer work of Adey and Burke (1976, 1977) and Adey (1986) on algal ridges, CCA have only rarely been used as paleo-RSL indicators in the western Atlantic and Caribbean Quaternary reefs. Martindale (1992) based on his own observations in modern reefs in Barbados (see above) interpreted thick crusts of *Porolithon* and *Lithophyllum* in Pleistocene reefs in the island as indicative of very shallow, high energy settings. Blanchon *et al.* (2002) report *Porolithon* and *Lithophyllum* associated with *A. palmata* in reef-crest deposits (< 5 m depth) in the Holocene of Grand Cayman. In the Holocene of Yucatan, Blanchon and Perry (2004) interpret *A. palmata* branches encrusted by cm-thick CCA, especially *Porolithon*, as indicative of reef crest/flat facies formed in less than 2 m depth, according to their own observations in the nearby modern reef. Blanchon and Eisenhauer (2001) and Blanchon *et al.* (2009) report an encruster association of thick CCA, vermetids, and the foraminifer *Homotrema rubrum* as a very shallow (< 1 m) facies in the LIG deposits of Barbados and Yucatan, respectively. In Saint Croix, Virgin Islands, also in LIG deposits Toscano *et al.* (2012) include crusts of CCA and *H. rubrum* as indicators of shallow water (< 5 m)(see Supplementary table).

Indo-Pacific

Modern

Davies and Montaggioni (1985) suggested that CCA ridges mainly formed by *P. onkodes* and *Porolithon gardineri* are precise indicators of mean low water springs (± 0.5 m) in the Pacific Ocean. According to Adey (1986), mainly based on Adey *et al.* (1982), genera in Indo-Pacific CCA assemblages show distributions similar to those in

the Caribbean. *Porolithon* and *Neogoniolithon* dominate assemblages in less than 10 m (Table 1). *Neogoniolithon* (including *Paragoniolithon*) replaces *Porolithon* down to 20-25 m, and *Hydrolithon* dominates assemblages deeper than 30 m; *Lithothamnion, Mesophyllum* and *Sporolithon* (as *Archaeolithothamnium*) are the most common CCA below 50 m. In the Ryukyu Islands, Iryu *et al.* (1995) recorded a dominance of *Porolithon onkodes* (as *Hydrolithon onkodes*), *Lithophyllum* and *Dawsoniolithon conicum* (as *Neogoniolithon conicum*) in the upper 10 m. The proportion of *Neogoniolithon* substantially increases from 10 to 20 m, and *Hydrolithon* and *Mesophyllum* mainly occur below 20 m.

Cabioch *et al.* (1999) considered thick crusts of *Porolithon* cf. *onkodes* (as *Hydrolithon*) and *Neogoniolithon* cf. *fosliei* characteristic of depth less than 6 m (Table 1), whereas thinner crusts dominated by *Lithophyllum* and *Mesophyllum* would indicate depths of 6-15 m (see Supplementary table). Additional data on species depth distributions were published in accounts of local CCA assemblages (for example CCA on Heron Reef in the Great Barrier Reef, Ringeltaube and Harvey, 2000), and algal guides such as the one of Payri *et al.* (2000) for French Polynesia, and Littler and Littler (2003) for South Pacific reefs.

Rasser and Piller (1996; 1997) recognized a different CCA assemblage as potential paleodepth indicator in living reefs in the northern Red Sea. These authors observed an association of *Lithophyllum kotschyanum*, together with *P. onkodes* (as *Hydrolithon*) and *Neogoniolithon brassica-florida* encrusting corals, forming rhodoliths or frameworks on the intertidal or shallow subtidal reef flat. Another association, characterized by *P. onkodes* extends down to 15 m (Rasser and Piller, 1997).

Among the facies recognizable in the Indo-Pacific coral reefs, Montaggioni (2005) distinguished a "Coralline algal facies" formed by crusts of *P. onkodes* (as *Hydrolithon*), *Neogoniolithon* spp., *Mesophyllum* sp. and *Lithophyllum* sp., associated with encrusting foraminifers, vermetid gastropods and serpulids. The crusts can reach up to 2 m in thickness in windward reef crests and flats, and lagoonal patches exposed

to high turbulence, being thinner in more sheltered areas. According to Montaggioni (2005), *Porolithon* cf. *onkodes* also forms thick crusts in the "Robust-branching coral facies" typical of depths shallower than 6 m, and CCA crusts 1–10 cm thick occur in windward reef flats of the "Domal coral facies". Montaggioni and Braithwaite (2009) include calcareous alga-dominated communities equivalent to the "Coralline algal facies" of Montaggioni (2005) in their zonation scheme of Indo-Pacific reefs.

Molecular work suggests that at least 20 distinct cryptic CCA species are passing under the name *Porolithon onkodes* following morphological diagnostic characters (Gabrielson *et al.*, 2018). Nevertheless, in the Indo-Pacific the available data on *P. onkodes* distribution reflect the distribution of CCA with a morphoanatomy traditionally included in *P. onkodes* (herein referred as *Porolithon* gr. *onkodes*), characterized by smooth encrusting plants with common horizontal fields of trichocytes becoming buried in the thallus (Maneveldt & Keats, 2014).

According to the OBIS records, the probability depth distribution of *P. onkodes* is log-normal with most records at 0 m depth and with a 95 % being shallower than 0.2 m (Table 3, Fig. 4). This distribution, however, is probably biased by disproportionate dominance of shallow water surveys. In one of the few quantitative analyses of CCA distributions, Dean *et al.* (2015) only acknowledge a small effect of depth on composition of CCA assemblages on the Great Barrier Reef. However, they report that relative proportions of *P. onkodes* decreases from around 51 % of total CCA species in sites shallower that 5 m to 14 % below this depth, with no further data on depth ranges of the species.

In a systematic sampling of CCA both in the windward and leeward sides of One Tree Reef (GBR), *P.* gr. *onkodes* ranges from 1 to 27.5 m below mean sea level (median: 3.6 m, mean: 4.7 m ± 4.1 sd, Dechnik *et al.*, 2017). The theoretical log-normal distribution based on 124 samples indicates that 95 % of samples are shallower than 10.5 m. However, if only thick plants (thicker than 0.2 mm) are considered, as it is the

common procedure in paleo-RSL estimates, 95 % of samples are shallower than 8.8 m (data from Dechnik *et al.*, 2017) (Table 3, Fig.4).

Porolithon craspedium, whose common depth range according to phycologists is shallower than 20 m (Littler & Littler, 2003; Maneveldt & Keats, 2016), in the OBIS database (as *Hydrolithon craspedium*) is only reported below 30 m (32.5-46.5 m range, average 41.3 m ± 4 sd) (Table 3, Fig. 4). This example and the biased record of *P.* gr. *onkodes* suggest that the OBIS records of CCA species are questionable, probably due to the extreme difficulty of *in situ* identification of CCA taxa. The external morphology of many species is convergent and without the aid of a hand lens, and in many cases of optical or scanning electron microscopy no confident identification is possible.

Regarding CCA species that are characteristic or secondary components of assemblages with wider depth ranges, OBIS data on their depth distributions with statistical significance are very scarce. Among the few taxa with more than 30 records, *Melyvonnea erubescens* was found in the upper 20 m, whereas *Hydrolithon boergesenii* extends down to 80 m (Fig. 4). According to the OBIS database *Lithophyllum* gr. *prototypum* is restricted to 0 m. However, this species and species that can be included in this species group, such as *Titanoderma tessellatum,* have been observed at greater depths (down to 40 m, Littler and Littler, 2003). *Dawsoniolithon* gr. *conicum*, with no significant OBIS data, on One Tree Reef ranges down to 27 m, with maximum frequency from 10 to 20 m (as *'Pneophyllum' conicum*, Dechnik *et al.*, 2017) (Fig. 4).

Fossil

Pirazzoli and Montaggioni (1988) used the occurrence of *Porolithon onkodes* and *Neogoniolithon fosliei* to support their interpretation of massive branching *Acropora* facies with vermetids as a shallow water (< 3 m) indicator in Tahiti Holocene reefs. In these same reefs, Montaggioni *et al.* (1997) include thick crusts (> 2 cm) of *Porolithon onkodes* and minor *Neogoniolithon fosliei* as diagnostic components of the shallow

water (< 6 m) coralgal assemblage (robust branching community). Thinner crusts of *Neogoniolithon, Lithophyllum* (also as *Dermatolithon*), and *Lithothamnion* (as *Mesophyllum prolifer*) species would prevail in deeper assemblages with rare or absent *P. onkodes* (Supplementary table).

Thick crusts of *P. onkodes* (as *Hydrolithon onkodes* in several papers) have been considered the main component (and diagnostic) of CCA assemblages characteristic of shallow water depths (< 10 m) in a number of papers dealing with Indo-Pacific Quaternary records based either on samples collected on the seafloor (Camoin *et al.*, 2004; Webster *et al.*, 2004b; a, 2006, 2009; Cabioch *et al.*, 2008; Sanborn *et al.*, 2017; Hallmann *et al.*, 2020) or from drill cores (Camoin *et al.*, 2001, 2004, 2012; Cabioch *et al.*, 2003; Braga & Aguirre, 2004; Abbey *et al.*, 2011; Dechnik *et al.*, 2015, 2017; Gischler *et al.*, 2016, 2018b; a; Webster *et al.*, 2018; Yokoyama *et al.*, 2018; Humblet *et al.*, 2019; Montaggioni & Martin-Garin, 2020). In other cases, *P. onkodes* was considered indicative of a wider depth range (0-20 m, Iryu *et al.*, 2010) (Supplementary table).

Frameworks of branching *L. kotschyanum* have been interpreted as indicative of very shallow subtidal paleoenvironments in Pleistocene (MIS 7 and 5) reefs in the Danakil Depression, Afar, Ethiopia, a basin connected to the Red Sea in its Quaternary evolution (Jaramillo-Vogel *et al.*, 2019).

The paleowater depth to be interpreted from all *in situ* CCA fossil assemblages is the shallowest depth range of the co-occurring species. When the framework substrate on which they grew is overshadowed by new coral growth, shallow-water species that grew on well-illuminated surfaces can be overgrown by species characteristic of less illuminated habitats, which are the same as the deeper ones as light intensity is a major controlling factor on CCA distribution (Martindale, 1992; Abbey *et al.*, 2011).

Vermetids

Vermetids (Family Vermetidae, Class Gastropoda) include species of sessile, suspension-feeding, irregularly coiled marine snails living in warm temperate and tropical oceans (Golding *et al.*, 2014). They attach to hard substrates, including CCA, dead and living coral (Fig. 5), and have deleterious effects on reef building corals by reducing their skeletal growth and survival (Zvuloni *et al.*, 2008; Shima *et al.*, 2010, 2013).

Laborel (1986) presented an exhaustive synthesis of the applicability of vermetid bioconstructions as RSL indicators. However, these bioconstructions, which are precise markers of upper subtidal to low intertidal transition, usually form on rocky shorelines and do not develop on actively growing coral reefs. In coral reefs, vermetids attach to hard substrates commonly encrusting CCA but they remain as secondary components of the reef-building, encrusting community.

Atlantic/Caribbean

Modern

The gregarious vermetid *Dendropoma corrodens* is an abundant component in rims of cup reefs and constructional lips that develop at mean low tide level in Bermuda. *Dendropoma* densities are about 3000 individuals/m^2 in average with a high variance (Thomas & Stevens, 1991) (Table 1).

Dendropoma sp. was identified as the most abundant framework builder after CCA in the raised reef rim both in the windward and leeward sides of Atol das Rocas in Brazil (Gherardi & Bosence, 2001). In the fringing reefs of Abrolhos Archipelago in the eastern Brazilian shelf, '*Dendropoma*' *irregulare* (uncertain generic placement = *Vermetus irregularis*, Golding *et al.*, 2014) is an important component, together with *Porolithon antillarum* (as *P. pachydermum*) of reef edges, which at high tide have an average depth of 2 m and are subaerially exposed at low tide (Tâmega *et al.*, 2014; Spotorno-Oliveira *et al.*, 2015) (Table 1).

Fossil

In the Caribbean, the occurrence of abundant *Dendropoma* was used by Blanchon and Eisenhauer (2001) as indicative of paleodepths of < 1m (lower quarter of tidal range) in LIG deposits (*A. palmata* rudstone) from Barbados. The presence of vermetids and CCA and the foraminifer *H. rubrum* encrusting clasts of *A. palmata* was also considered characteristic of mean lower water in MIS 5e reefs from Yucatán (Blanchon *et al.*, 2009). Dechnik *et al.* (2019) suggest a paleodepth of < 1m for corals heavily encrusted by thick CCA and vermetids in the Holocene reefs in eastern Brazil (Supplementary table).

Indo-Pacific

Modern

In their comprehensive work on coralgal assemblages of the Indo-Pacific as RSL indicators, Cabioch *et al.* (1999) suggested that the vermetids *Dendropoma maximus*, currently named *Ceraesignum maximum*, and *Serpulorbis annulatus* are commonly associated with the robust branching coral facies, and can be considered indicative of depths shallower than 5 m (Table 1). The name *Serpulorbis annulatus* is not currently accepted; the specific name *annulatus* is either applied to serpulid worms in the genus *Filogranula* (*F. annulata*) or considered synonym of *Dendropoma corrodens*. However, none of those taxa occur in the Pacific (WoRMS, World Register of Marine Species, 2021). According to Cabioch *et al.* (1999), the assemblage robust branching coral/*Porolithon* (as *Hydrolithon*)/vermetids (Reef edge -RE- assemblage) is characteristic of near-surface environments, < 6 m. Montaggioni (2005) and Montaggioni & Braithwaite (2009) describe the association of vermetids with CCA in the "coralline algal facies" in reef crests and reef flats. Montaggioni (2005) also refers to the abundance of vermetids in the robust-branching coral facies, characteristic of high-energy setting (0-6 m), and in the heavily encrusted subfacies of the domal coral facies, developing in windward reef flats (Table 1).

Depth distributions of living vermetids listed in OBIS seem to question the use of their occurrence as indicator of very shallow water depth. Although members of the family Vermetidae have been mainly recorded in the shallower 20 m, they are most frequent from 10 to 20 m, and extend down to depths of hundreds of meters (Table 3, Fig. 6). The genus *Dendropoma* mentioned as indicative of very shallow water was also most commonly identified from 10 to 20 m depth, both considering only the species currently included in the genus or taking into account other, such as *C. maximum*, that were included in the genus before relatively recent taxonomic revisions (Golding *et al.*, 2014). Individual species reported as restricted to 0-6 m, such as *C. maximum* (as *D. maximum*), for example in Cabioch *et al.* (1999), also have been mainly recorded below 10 m depth (Table 3, Fig. 6).

However, the OBIS inventories do not adequately reflect the abundance of the recorded taxa in the surveyed site, and, therefore, relying upon modern depth distributions registered in OBIS overlooks the role of organisms as facies builders/components and the environmental/paleoenvironmental significance of those facies. The vermetid formations in the low-intertidal/subtidal transition are well known in the Mediterranean, Brazilian and Caribbean shorelines (Laborel, 1986; Angulo *et al.*, 2006; Suguio *et al.*, 2013). In a similar way, *Dendropoma gregarium* forms benches in the intertidal zone in the Hawaiian Islands, with densities up to 60,000 individuals/m^2 (Hadfield *et al.*, 1972, as *D. gregaria*). However, the densities of non-gregrarious vermetids associated to coral reefs are much lower than those outstanding concentrations. In the Red Sea north of Jeddah (Saudi Arabia) densities about 22 individuals/m^2 of *C. maximum* (as *D. maximum*) characterize the outer reef flat (Hughes & Lewis, 1974). Also in the Red Sea, in the Gulf of Aqaba, the highest density of *C. maximum* was found on the upper 1 m of the vertical wall at the seaward margin of the reef flat. At this margin, the average density measured by Ribak *et al.* (2005) was 6 individuals/m^2 and increased to 14 individuals/m^2 in a later study in the same area by Zvuloni *et al.* (2008). *C. maximum* occurred on the reef flat and was rare in the shallow

lagoon but was absent deeper than 3 m (Ribak *et al.*, 2005). *C. maximum* (as *D. maximum*) is also nearly restricted to reef flats in the Bay of Sarfaga (Red Sea, Egypt) where it has average densities of 20 individuals/m^2, whereas its occurrence in other reef settings is anecdotal (Zuschin *et al.*, 2001). Average densities of 17 individuals/m^2 (up to 165/m^2) were observed at the top of patch reefs in the Moorea lagoon before a mass mortality in 2015 (Brown *et al.*, 2016). However, little information is available on how to translate surface densities observed in modern ecological surveys to individuals per volume or per area perpendicular to the depositional surface of reef framework, which is the common approach used in the observation of vermetids in drill cores and fossil reef outcrops (Fig. 5). In an attempt to provide this kind of information, in One Tree Reef vermetid abundance was estimated in line transects, perpendicular across the CCA crusts. Vermetid densities higher than 5 individuals/cm are restricted to the shallower 6 m, both in the windward and leeward sides (Dechnik *et al.*, 2017), supporting the use of vermetid abundance as a RSL indicator in the Great Barrier Reef Quaternary records.

In short, vermetid gastropods live in modern oceans in a wide depth range, and according to OBIS inventories no species is restricted to a narrow shallow-water zone. However, according to published records including abundance estimates mentioned above, relatively high densities of vermetids (> 10 individuals/m^2) in coral/CCA reef communities only occur in shallow depths, from above mean low tide to some 6 m depth.

Fossil

The occurrence of *Serpulorbis annulatus* (see comment above) in cores from Holocene reefs in Tahiti was used by Pirazzoli and Montaggioni (1988) to interpret paleodepths of less than 3 m (Table 1). In cores from deglacial and Holocene reefs in the same Tahitian locality, Bard *et al.* (1996) considered the assemblage of robust-branching corals, CCA and vermetids indicative of depths < 6 m. The abundance of

vermetids in association with *P. onkodes* has been considered evidence to support a

shallow paleodepth (less than 10 m, usually less than 6 m) in the interpretation of

coralgal assemblages from dill cores of Indo-Pacific Pleistocene and Holocene reefs

(Camoin *et al.*, 2001; Cabioch *et al.*, 2003; Abbey *et al.*, 2011; Deschamps *et al.*, 2012;

Dechnik *et al.*, 2015, 2017; Gischler *et al.*, 2016, 2018a; Webster *et al.*, 2018;

Yokoyama *et al.*, 2018; Humblet *et al.*, 2019, Supplementary table).

CONCLUDING REMARKS

      The validity of the coral assemblages as paleodepth indicators in Quaternary

reefs depends on the depth distributions of their modern component species. In the

Western Atlantic-Caribbean province *A. palmata* is the most precise RSL marker and

no assemblage approach improves its results (Hibbert *et al.*, 2016; Stathakopoulos *et

al.*, 2020).

      In the Indo-Pacific province, the available OBIS data on depth ranges of

component species support the use of two assemblages considered indicative of

narrow, shallow paleodepth ranges with a 10-m uncertainty. In the case of the robust-

branching assemblage (Table 1) many component species, such as *Acropora humilis,

A. aspera, A. nasuta, A. hyacinthus, A. lastitella, A. gemmifera*, and *A. palmerae*,

Isopora palifera, Pocillopora damicornis, Leptoria phrygia, Favites flexuosa, and

Goniastrea favulus have unimodal distributions, and median and average depths of

records shallower than 10 m (Table 2, Figs. 1, 7). An average of more than 80 % of

records of assemblage components are shallower than 6 m (Table 2, Figs. 1, 7).

According to their probability distributions, 95 % of the records of *A. hyacinthus*, *A.

latistella* and *G. favulus* are shallower than about 10 m.

      In the case of the high-energy subtype of the encrusting coral assemblage

(Montaggioni, 2005), according to OBIS data many of its species (*Acropora

microphthalma, Montipora monasteriata, M. danae, M. undata, Pachyseris speciosa,

Echinophyllia aspera*, *Echinopora lamellosa, Cyphastrea microphthalma, C. serailia,*

Merulina ampliata, and *Porites lutea*) are restricted to shallow depths, with modes and medians well above 10 m (Table 2, Figs. 2, 7). As an average, 73 % of records of the components of this assemblage are shallower than 6 m. In the case of *P. lutea* and *A. microphthalma*, 95 % of occurrence probability is shallower than 10 m (Table 2, Figs. 2,7). These overlapping mode, median and average depths suggest that both the robust-branching and the high-energy encrusting coral assemblages can be reliable indicators of paleodepths shallower than 10 m when identified by several species (Table 2, Fig. 7).

The reliability of the robust-branching and high-energy coral assemblages as indicative of shallow depths is reinforced when corals are associated with thick crusts of *P*. gr*. onkodes*. According to OBIS data CCA of this group are restricted to very shallow waters with theoretically 95 % of records shallower than 0.2 m and 99.6 % of records shallower than 6 m (Table 3, Figs. 4, 7)). However, these data and, in general, the few data concerning CCA species in OBIS are questionable due to either biased sampling or to difficulties of identifying CCA species without the aid of lab-based optical and electronic microscopy. Sampling and subsequent microscopical examination of living CCA on One Tree Reef indicates that *P*. gr. *onkodes* has a log-normal distribution with median depth of 3.5 m, 95 % of occurrence probability of thick crusts are shallower than 8.8 m, and 86.4 % of records are shallower than 6 m (Table 3, Figs. 4, 7).

The presence of relatively high densities of vermetids, common in shallow-water coralgal assemblages, seems to indicate paleodepths less than 6 m, but data on modern distributions of vermetid densities are scarce. In the OBIS database vermetid species are recorded in wide depth ranges (Table 3). However, when abundance of vermetid individuals is taken into account, relatively high densities (> 10 individuals/m^2 on coral and CCA surfaces and > 5 individuals/cm in CCA sections) only occur from above mean low tide to some 6 m depth.

The accurate use of coralgal and vermetid assemblages as RSL indicators requires the identification of fossil corals and CCA at the species or species-group level. There is need of studies on distributions of CCA species and vermetid in modern coral reefs worldwide (Woodroffe & Webster, 2014).

The coralgal approach would be reinforced by quantitative surveys of the modern reef ecology, including spatial distributions of coral and CCA species, as well as extensive information of the physical environment at locations close to the studied fossil reefs (Hongo & Kayanne, 2010; Dutton *et al.*, 2015; Hibbert *et al.*, 2016; Chutcharavan & Dutton, 2020). Comparison with modern depth distributions of nearby reef community components allows precising the depth ranges of fossil assemblages (Webster *et al.*, 1998; Sagawa *et al.*, 2001; Kayanne *et al.*, 2002; Sugihara *et al.*, 2003; Hongo & Kayanne, 2009, 2011; Dutton *et al.*, 2015; Vyverberg *et al.*, 2018). However, *a priori* there are no reasons to assume that past conditions, even in the Holocene, were the same as the present-day. Extensive sampling of fossil reefs with cores/sections distributed across different paleoenvironments, in parallel with the generation of dense chronologic data sets represents a robust strategy to understand fossil reef architecture, spatio-temporal variations in coralgal assemblages, and better assess their RSL significance.

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Figure Captions

Figure 1. Modern depth distributions for 16 Indo-Pacific coral species characteristic of the "Robust-branching coral assemblage" with gamma and unimodal theoretical depth distributions according to OBIS database (accessed October 2021). Species arranged according to family ascriptions. Depth bins= 1 m. Red lines: best fit distribution. See Table 2 for descriptive statistics.

Figure 2. Modern depth distributions for 16 Indo-Pacific coral species characteristic of the "High-energy encrusting coral assemblage" with gamma and unimodal theoretical depth distributions according to OBIS database (accessed October 2021). Species

arranged according to family ascriptions. Depth bins= 1 m. Red lines: best fit distribution. See Table 2 for descriptive statistics.

Figure 3. *Porolithon* gr. *onkodes*. A) thick crusts of *P*. gr. *onkodes* (pink to purple surfaces) covering dead coral and rubble with some branching plants of *Lithophyllum* gr. *kotschyanum* (green arrowheads). B) SEM image of plants from the same locality showing the main diagnostic morphoanatomical characters of *P.* gr. *onkodes*: uniporate conceptacles (red arrowheads) and fields of trichocytes (orange arrowheads). Leeward coralgal rim, One Tree Reef, southern Great Barrier Reef, Australia.

Figure 4. Modern depth distributions of coralline algal species common in coral reefs with enough data in the OBIS database (accessed October 2021) to be statistically significant, and distributions in One Tree Reef (OTR) of significant species according to Dechnik *et al.* (2017). Depth bins= 3 m. Red lines: best fit distribution. See Table 3 for descriptive statistics.

Figure 5. Vermetid gastropods (orange arrowheads) intergrown with coralline algae in leeward coral framework, Holocene, One Tree Reef, southern Great Barrier Reef, Australia.

Figure 6. Modern depth distributions of vermetid gastropod taxa used in paleo-RSL reconstructions in coral reefs. Depth bins= 3 m. Red lines: best fit distribution. See Table 3 for descriptive statistics.

Figure 7. Probability depth distributions of Indo-Pacific species (different color lines) with gamma and unimodal best fits characteristic of "Robust-branching" and "High-energy encrusting" coral assemblages according to OBIS data (accessed October 2021). Note the coincidence of mode and median depths (ranges of median depths in

pale brown rectangle) well above 10 m. Distribution of the CCA *Porites* gr. *onkodes* according to OBIS (accessed October 2021) and surveys by Dechnik *et al.* (2017) at One Tree Reef (OTR). Purple line marks the depth above which vermetid densities of > 10 individual/m^2 or > 5 individual/cm in line transects perpendicular to crusts have been reported in coral reefs.

Table captions

Table 1. Most precise paleo-RSL indicators according to literature on the distributions of modern coral, coralline algal and vermetid assemblages/taxa. Only the shallowest assemblages (< 10 m depth) of each group are included. See Supplementary table for information on deeper assemblages in the literature. Taxonomic names in brackets reflect later modifications of the nomenclature by Huang *et al.* (2014) for the families Merulinidae, Montastraeidae, and Diploastraeidae, Huang *et al.* (2016) for the Lobophylliidae, and Veron (2000) for other families. MLSL: mean low sea level; MHSL: mean high sea level.

Table 2. Modern depth range, average depth of Indo-Pacific coral species characteristic of the "Robust-branching" and "High-energy encrusting" coral assemblages (Montaggioni, 2005) with gamma and unimodal best-fit probability distributions. Species arranged according to family ascriptions. Data from OBIS (accessed October 2021). The species depth-range in the IUCN database are also included.

Table 3. Modern depth range, median depth, and depth for maximum 95 % confidence interval (95 % shallower records) of coralline algal species common in coral reefs with enough data for statistical analysis in the OBIS database (accessed October 2021), and distributions in One Tree Reef (OTR) of significant species according to Dechnik *et*

al. (2017). Vermetid taxa used as paleo-RSL indicators in coral reefs with enough data for statistical analysis in OBIS (accessed October 2021).
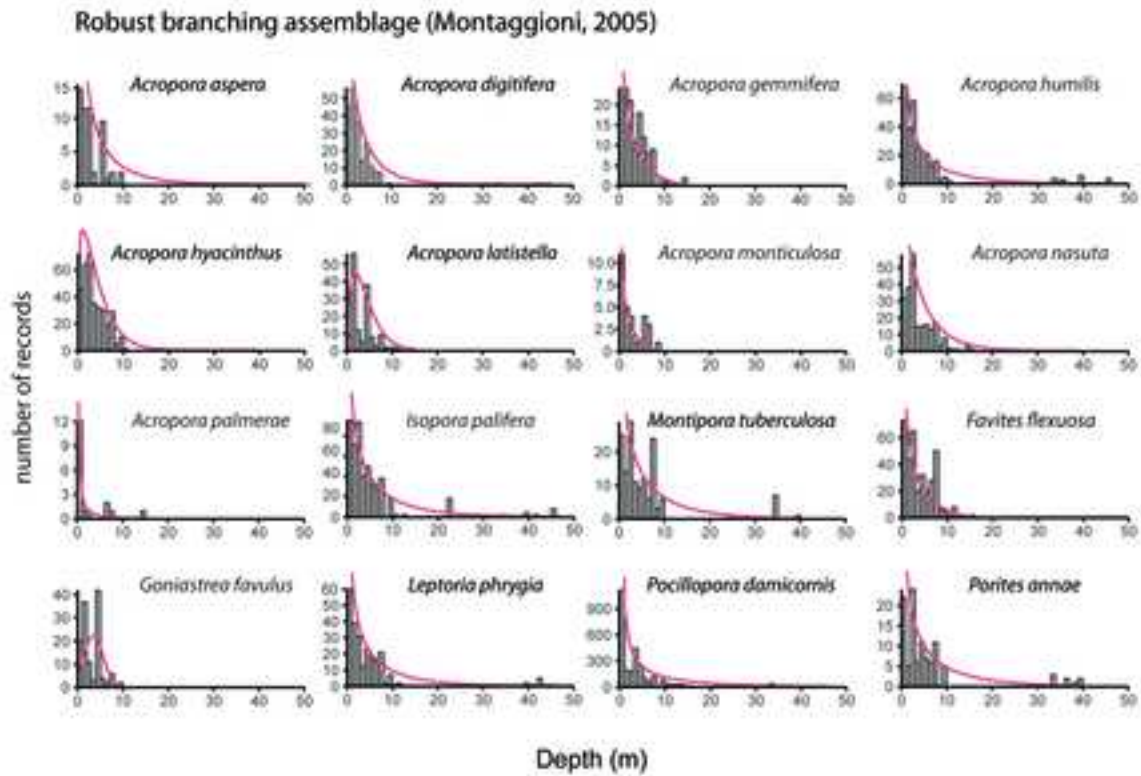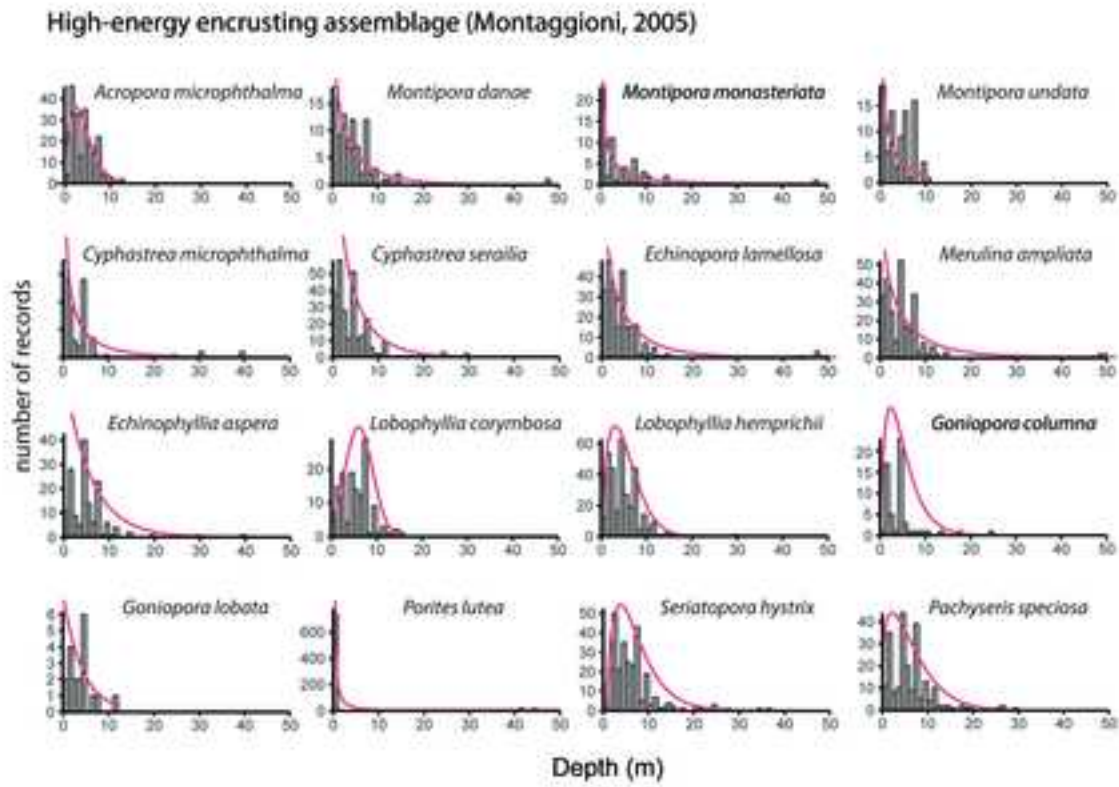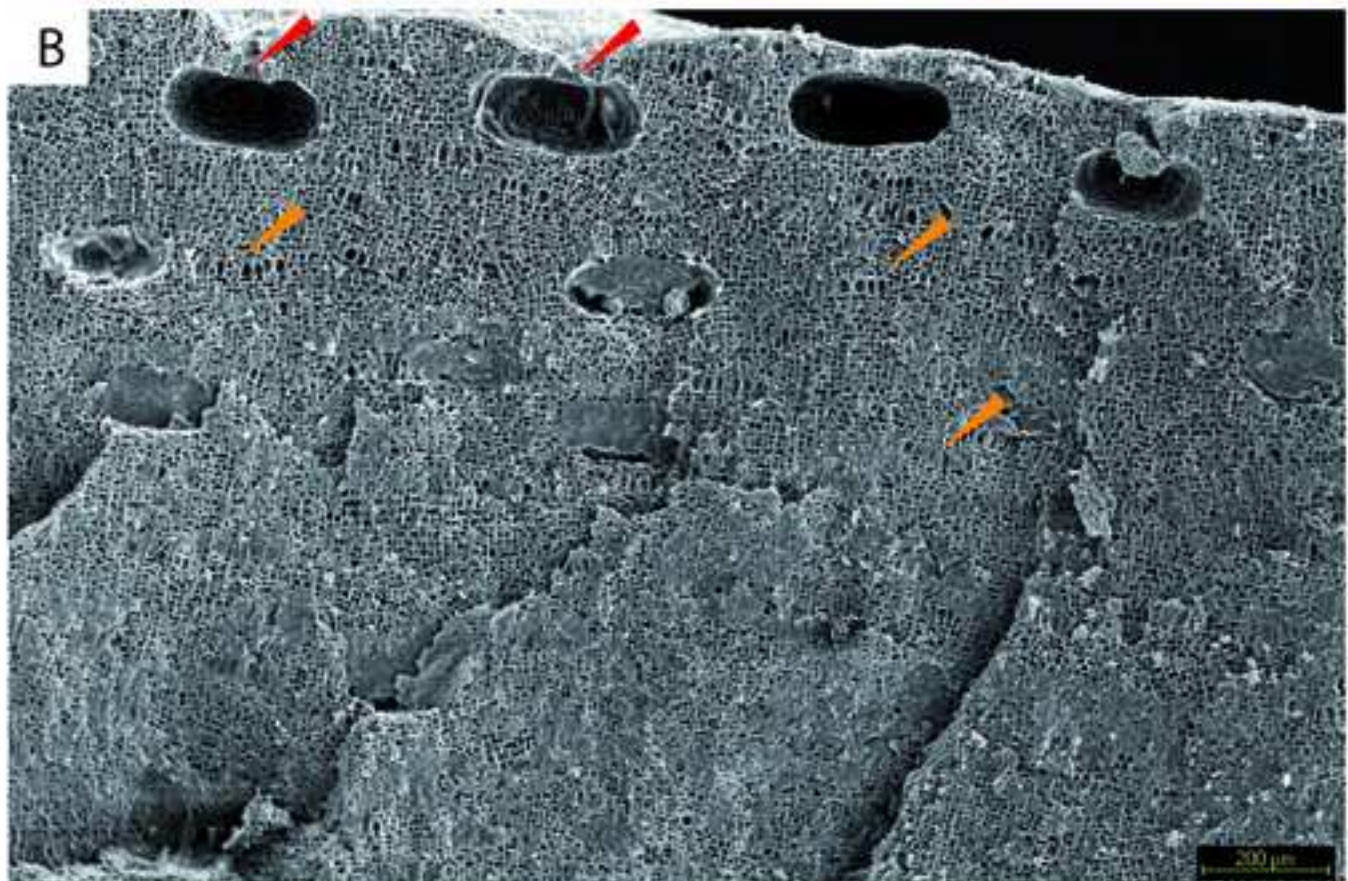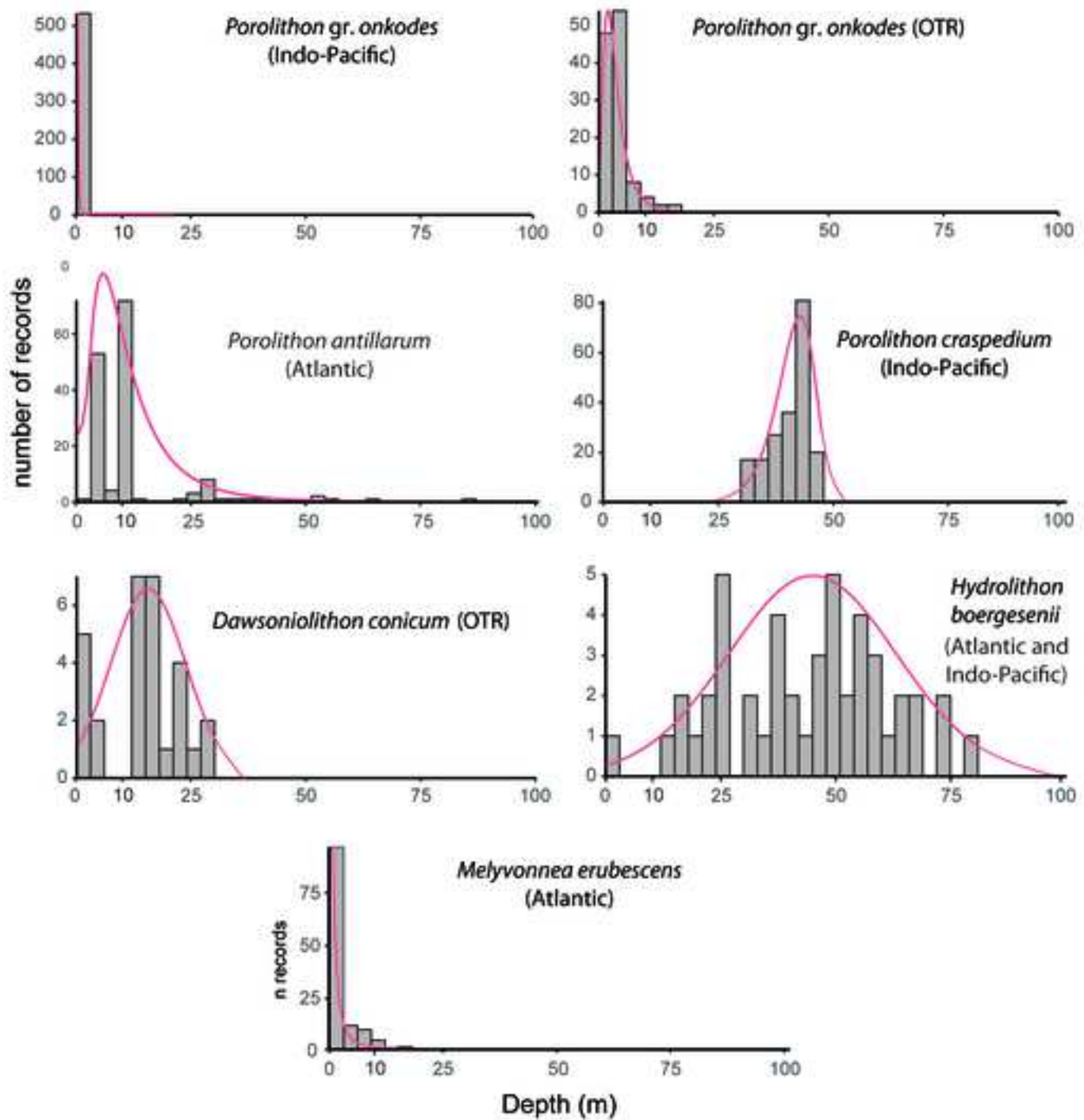
Figure 1

High-energy encrusting assemblage (Montaggioni, 2005)

Depth (m)

Figure 2

Figure 3

Figure 4
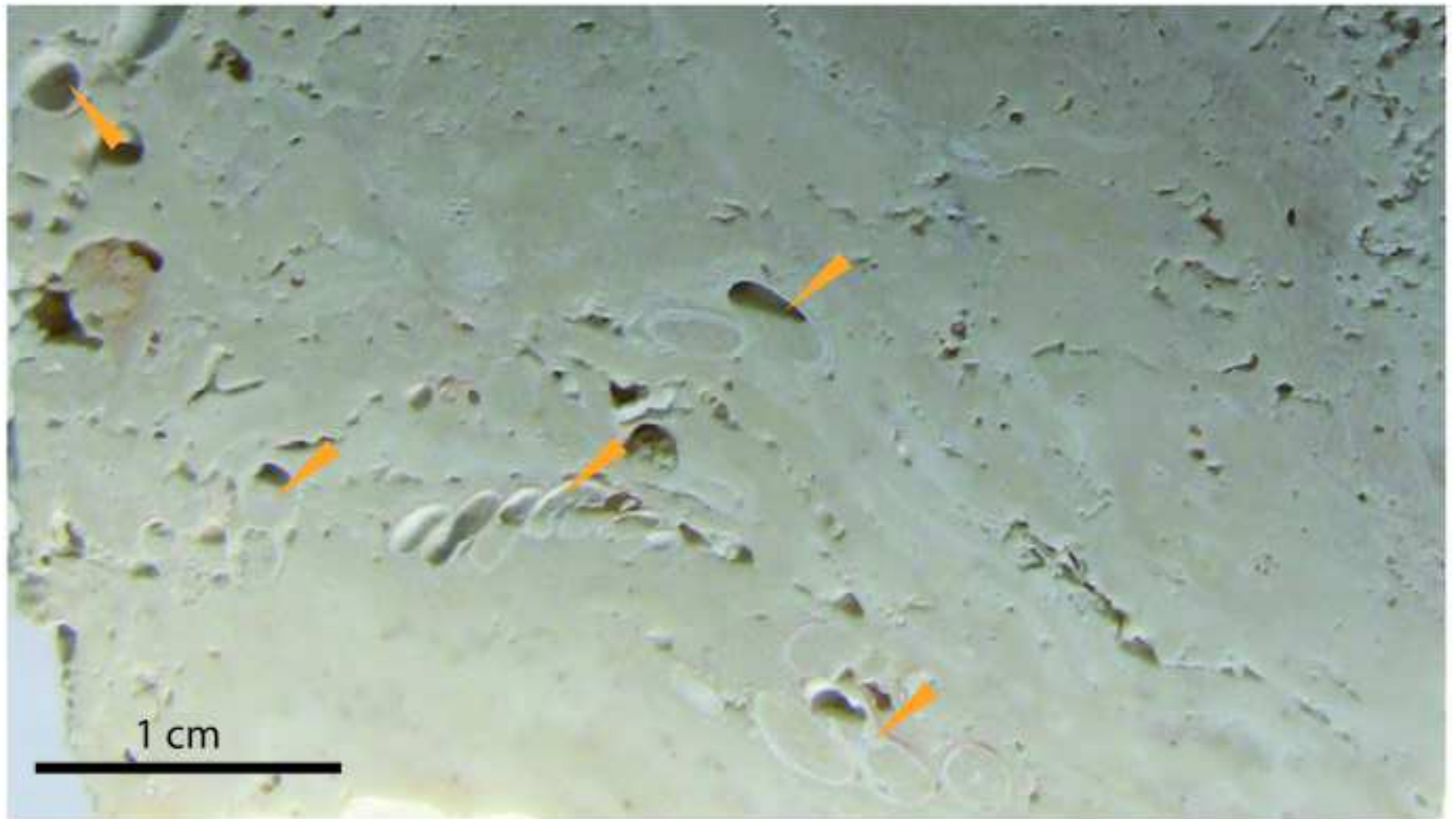
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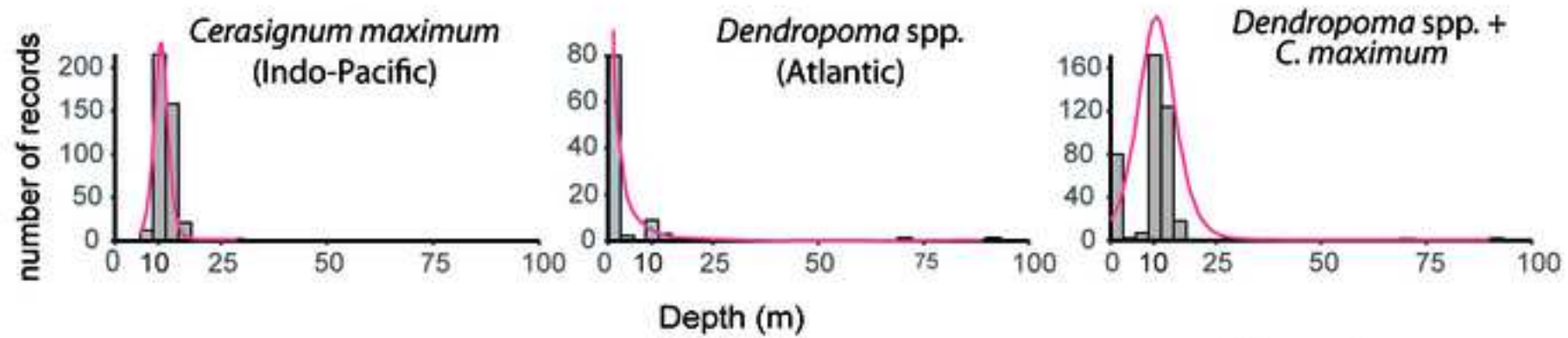
Figure 6
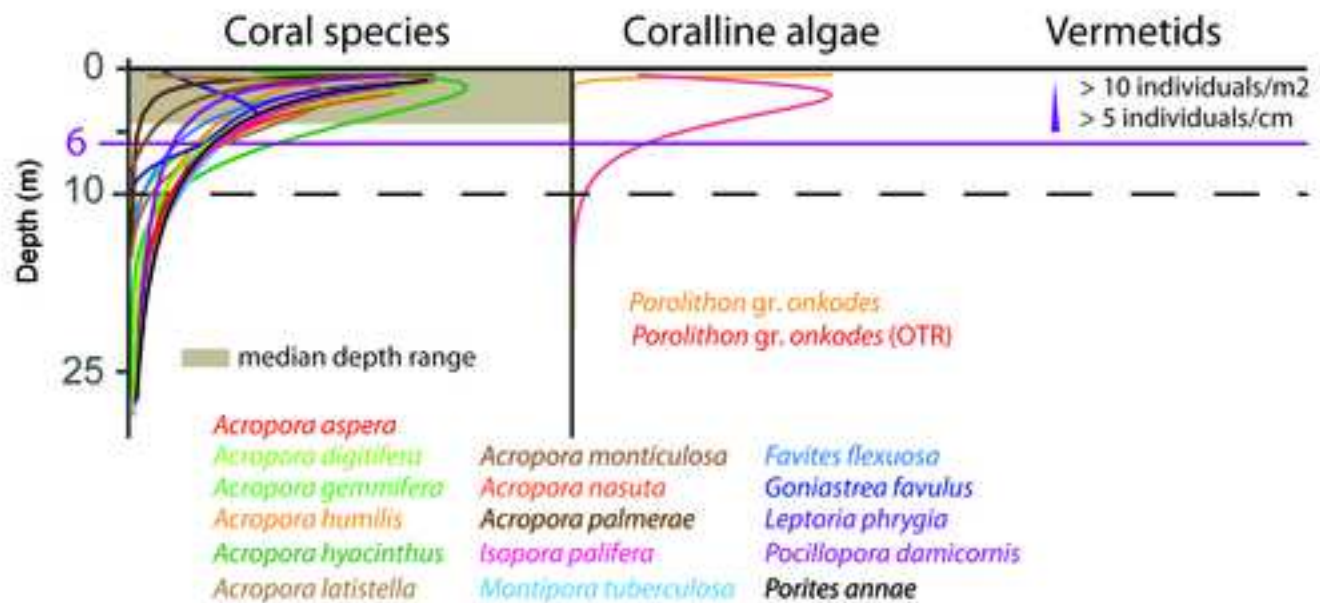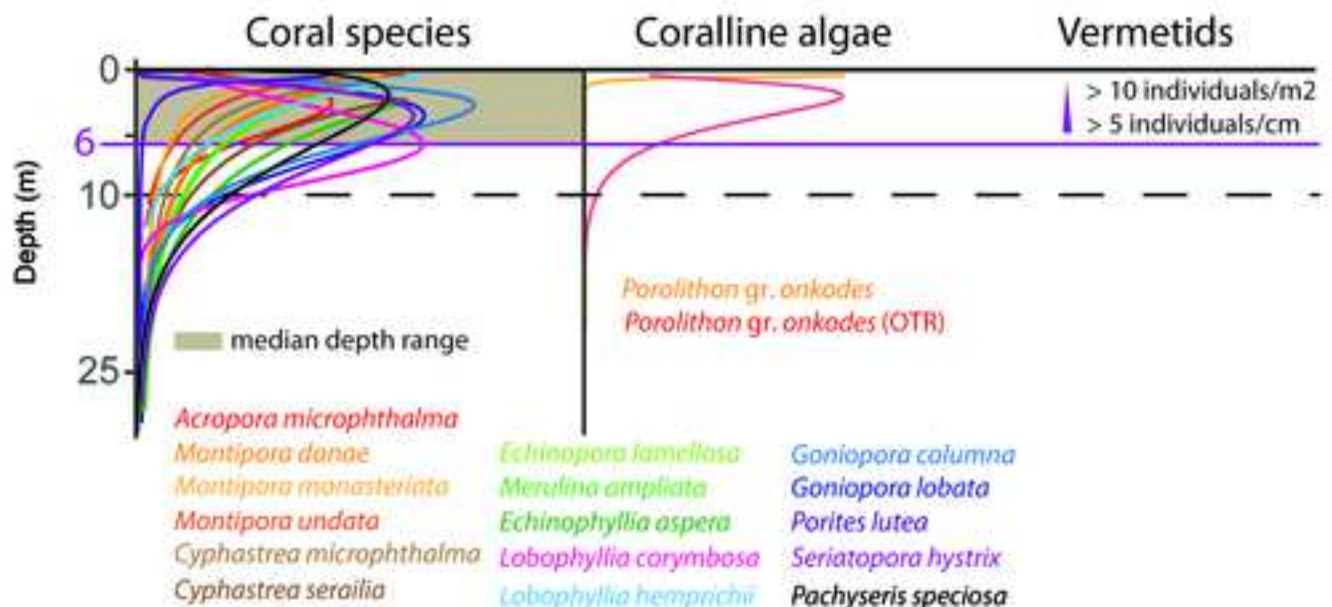
Figure 7

Coral assemblages	Depth range	Environment	References
Atlantic/Caribbean			
Acropora palmata	0-5 m	High-energy reef crest	Lighty *et al.,* 1982; Hibbert *et al.,* 2016, 2018
Indo-Pacific			
Robust-branching coral assemblage. Charecterised by *Acropora* gr. *robusta: A. robusta, A. danai* (= *A. abrotanoides*)*, A. abrotanoides, A. palmerae; Acropora (Isopora) palifera; A.* gr. *humilis: A. humilis, A. digitifera, A. gemmifera*)*; A. latistella*, and pocilloporids (*Pocillopora damicornis, P. eydouxi* (=*P. grandis), P. verrucosa, P. meandrina, Stylophora pistillata, S. mordax* (= *S. pistillata*). Subordinate associated domal (*Porites lutea, P. lobata, Leptoria phrygia, Platygyra daedala, Goniastrea retiformis, Goniastrea favulus, Favia stelligera* (= *Goniastrea stelligera*)*, Favia* (= *Dipsastraea*) *spp., Psammocora* sp., *Astreopora* sp., *Montipora* sp., platy (*Millepora platyphylla*), tabular (*A. hyacinthus*), columnar (*Porites annae*) and encrusting (*Montipora tuberculosa, Echinopora gemmacea*) assemblages.	0–6 m	High-energy, windward margins (upper forereef to outer reef flat zones)	Montaggioni, 2005, Montaggioni & Braithwaite, 2009
High-energy encrusting coral assemblage. According to the region considered, this may include the acroporids *Montipora monasteriata, M. capitata, M. undata, M. patula, M. danai*, the agariciids *Leptoseris mycetoseroides*, *Pachyseris speciosa*, the pectiniid (= lobophylliids) *Echinophyllia aspera*, the faviids (= incertae sedis) *Leptastrea purpurea*, (merulinids) *Echinopora lamellosa, E. gemmacea, Cyphastrea serailia, C. microphthalma, C. ocellina*, the poritid *Alveopora daedala*, the merulinid *M. ampliata*; may be mixed with dome-shaped faviids (= merulinids), i.e.*F.* (= *D.*) *pallida, F.* (= *D.*) *speciosa, Oulophyllia crispa*, acroporids, i.e. *A. myriophthalma, Astreopora ocellata, Astreopora* spp., poritids, i.e. *Porites lutea, P. lobata, Goniopora lobata, G. columna*), mussids (= lobophylliids) (*Lobophyllia corumbosa, L. hemprichii, Acanthastrea echinata*), associated with finely branching (*Acropora echinata, Seriatopora hystrix*) or with meandroid forms (*Plerogyra sinuosa*). Also free-living corals (*Fungia* spp., *Halomitra* sp., *Herpolitha* sp.).	0-10 m	High-energy reef crests, outer and inner slopes of ocean-facing fringing reefs, mid- to inner-shelf reefs	

Coralline algal assemblages

Atlantic/Caribbean

Porolithon antillarum (as *Porolithon pachydermum*) and *Lithophyllum kaiseri* (as *Lithophyllum congestum*)	0-3 m 0-6 m	High energy reef crest	Martindale, 1992 Adey, 1986
Extensive framework of algal ridge	close to/slightly above MLSL		Adey and Burke, 1976, 1977
Porolithon gr. *onkodes, Melyvonnea erubescens* (as *Mesophyllum erubescens*)	2-5 m		Jesionek *et al.*,2016; Amado-Filho *et al.*,2018

Indo-Pacific

P. onkodes and *Neogoniolithon*	0-10 m		Adey, 1986; Iryu *et al.* 1995
P. onkodes (as *Hydrolithon onkodes*) and *Neogoniolithon*	0-6 m		Cabioch et al. 1999

Vermetids

Atlantic

Dendropoma corrodens	MLSL	Rims of cup reefs Bermuda	Thomas and Stevens, 1991
Dendropoma sp.	Above MHSL	Raised reef rim Atol das Rocas	Gherardi and Bosence, 2001
Vermetus irregularis (as *'Dendropoma irregulare'*	Intertidal	Reef edge Abrolhos	Tamega *et al.,* 2014; Spotorno-Oliveira *et al.,* 2015

Indo-Pacific

Ceraesignum maximum (as Dendropoma maximus)	0-6 m	Upper forereef to outer reef flat zones	Cabioch *et al.,* 1999; Montaggioni, 2005; Montaggioni and Braithwaite, 2009
Densities of *Ceraesignum maximum* > 10/m^2	0-6 m	Reef flat and upper foreref	Hughes and Lewis, 1974; Zvuloni *et al.* (2008); Zuschin *et al.*, 2001

Coral species	Number of observations	Min. Depth (m)	Max. Depth (m)	Mean (m)	Median (m)	SD	Value at 95 percentile (m)	% records shallower than 6 m	Records shallower than 6 m	Best Fit Distribution	IUCN depth range (m)
Robust branching assemblage											
Acropora aspera	57	0,0	65,0	4,2	3,0	8,6	16,2	89,5	51	gamma	0-5
A. digitifera	208	0,0	45,0	3,8	3,0	5,8	13,0	89,9	187	gamma	0-12
A. gemmifera	131	0,0	15,0	3,9	4,0	3,0	13,6	82,4	108	gamma	1-15
A. humilis	300	0,0	46,0	6,4	3,0	10,0	24,9	78,0	234	gamma	0-11
A. hyacinthus	344	0,0	38,5	4,1	3,0	3,2	10,8	81,1	279	Weibull	5-20
A. latistella	148	0,0	15,0	4,0	3,0	2,6	9,5	86,5	128	Weibull	3-20
A. monticulosa	30	0,0	9,0	2,9	2,0	2,8	11,9	86,7	26	gamma	1-12
A. nasuta	225	0,0	60,0	4,5	3,0	4,9	14,3	77,3	174	gamma	3-15
A. palmerae	18	0,0	15,0	2,4	0,0	4,2	15,5	77,8	14	log-normal	0-12
Isopora palifera	254	0,0	46,0	5,8	3,0	8,2	20,9	75,6	192	gamma	2-20
Montipora tuberculosa	148	0,0	40,0	6,1	4,0	7,8	22,8	67,6	100	gamma	0-40
Favites flexuosa	194	0,0	16,0	4,0	3,0	3,3	15,0	73,2	142	gamma	1-20
Goniastrea favulus	128	0,0	10,0	3,5	3,0	2,3	7,3	91,4	117	normal	0-15
Leptoria phrygia	240	0,0	54,0	5,3	3,0	8,5	20,9	75,8	182	gamma	0-30
Pocillopora damicornis	2954	0,0	98,0	6,7	3,0	14,5	31,3	77,6	2292	gamma	1-20
Porites annae	105	0,0	40,0	6,5	4,0	9,2	25,3	71,4	75	gamma	0.5-30
High-energy encrusting assemblage											
Acropora microphthalma	201	1,0	13,0	4,8	5,0	2,6	9,7	74,1	149	gamma	5-20
Montipora danae	90	0,0	48,0	5,0	4,0	5,8	18,4	73,3	66	gamma	0-40
Montipora monasteriata	62	0,0	48,0	4,7	3,0	6,9	20,9	72,6	45	gamma	1-40
Montipora undata	87	0,0	11,0	4,3	5,0	3,1	16,4	74,7	65	gamma	2-30
Cyphastrea microphthalma	109	0,0	40,0	4,1	2,0	7,0	17,7	87,2	95	gamma	0-30
C. serailia	263	0,0	30,0	4,9	4,0	4,8	16,3	74,9	197	gamma	0-50
Echinopora lamellosa	245	0,0	52,0	5,5	4,0	7,9	18,9	76,3	187	gamma	1-40
Merulina ampliata	257	0,0	52,0	5,8	5,0	7,3	20,0	69,3	178	gamma	0-50

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Echinophyllia aspera	154	0,0	60,0	6,0	5,0	6,5	17,9	69,5	107	exponential	3-40
Lobophyllia corymbosa	136	0,0	16,0	6,0	6,0	3,2	11,3	55,9	76	normal	2-40
L. hemprichii	317	0,0	30,0	5,4	5,0	3,3	12,0	68,1	216	Weibull	1-50
Goniopora columna	58	0,0	24,3	5,0	5,0	4,0	12,0	86,2	50	gamma	2-15
G. lobata	19	0,0	12,0	4,2	4,0	2,8	12,5	84,2	16	exponential	2-10
Porites lutea	877	0,0	52,0	5,9	0,0	14,7	4,6	85,6	751	log-normal	0-30
Seriatopora hystrix	286	0,0	62,0	6,8	6,0	6,1	16,4	57,7	165	gamma	1-20
Pachyseris speciosa	223	0,0	30,0	6,6	6,0	4,7	16,6	57,4	128	Weibull	4-25

Taxon	Number of observations	Min. Depth (m)	Max. Depth (m)	Mean (m)	Median (m)	SD	Value at 95 percentile (m)	% records shallower than 6 m	Records shallower than 6 m	Best Fit Distribution
Coralline Algae										
Hydrolithon boergesenii (Atlantic and Indo-Pacific)	47	0,0	79,0	44,1	46,0	18,2	73,6	2,1	1	normal
Porolithon craspedium (Indo-Pacific)	198	32,0	48,0	41,3	42,5	4,0	46,5	0,0	0	Weibull
Porolithon antillarum (Atlantic)	153	2,0	85,0	12,4	10,5	12,4	29,1	35,3	54	log-normal
Porolithon onkodes (Indo-Pacific)	536	0,0	19,0	0,1	0,0	1,0	0,2	99,6	534	log-normal
Melyvonnea erubescens (Atlantic)	121	0,0	17,0	2,0	0,5	3,2	5,5	88,4	107	log-normal
Coralline Algae One Tree Reef										
Dawsoniolithon conicum (OTR)	29	0,0	27,4	14,3	16,4	7,8	27,1	24,1	7	normal
Porolithon onkodes (OTR)	118	1,0	16,6	4,1	3,5	2,8	8,8	86,4	102	log-normal
Vermetids										
Ceraesignum maximum (Indo-Pacific)	310	8,0	28,0	12,6	12,0	1,9	15,1	0,0	0	logistic
Dendropoma spp. (Atlantic)	97	0,0	91,0	3,9	0,8	12,1	9,7	85,6	83	log-normal
Dendropoma spp. (incl. *C. maximum*)	406	0,0	91,0	10,5	12,0	7,1	19,8	20,4	83	logistic

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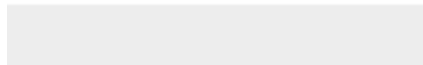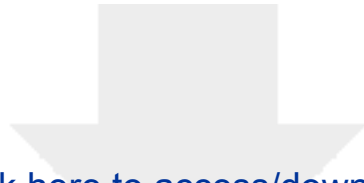
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