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ORIGINAL PAPER

Upper Pleistocene cold-water corals from the Inner Sea of the Maldives: taphonomy and environment

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Abstract Cold-water corals of the Late Pleistocene (21,400–22,500 BP) are recorded from the sea-bottom of two inter-atoll channels (Kardiva Channel at 457-m depth and Malé Vaadhoo Channel at 443-m depth) of the eastern row of the Maldives archipelago. Coral assemblages are composed mainly by *Lophelia pertusa* and secondarily by *Madrepora oculata* and *Enallopsammia rostrata*. These cold-water coral patches are places where the benthic life, mainly sessile, is concentrated, which is clearly absent off-rubble patches. The main epibionts are tube-dwelling polychaetes (mainly *Spirorbis* and *Serpula*), bryozoans, siliceous sponges, barnacles, gorgonids, solitary corals, encrusting foraminifera, and microbial mats. The analysis of epibionts assemblages shows different biocoenoses between both studied sites as well as a dependency of the epibiont coverage with regard to the coral genus. Some living benthic organisms such as brachiopods, bivalves, gastropods, barnacles, and ophiuroids find refuge among coral branches. The common record of juvenile specimens of vagile organisms such as small ophiuroids, is probably related to the nursery function of the cold-water corals in spite they are fossils. Environmental requirements of Recent cold-water corals (*Lophelia*, *Madrepora* and *Enallopsammia*) differ of conditions at both sampling sites with sensibly lower oxygenation degree and density of waters than needed for cold-water corals. Therefore, it is proposed that the present-day oxygen and density conditions are the factors which inhibit modern cold-water coral growth in the inter-atoll channels.

Keywords *Lophelia* · Coral rubble · Epibionts · Oxygenation · Indian Ocean

Introduction

Cold-water coral buildups host communities of associated animals that are distinct from the surrounding background deep-sea fauna and have high species diversity and sometimes a high level of endemism (Henry and Roberts 2007; van Soest et al. 2007; Mastrototaro et al. 2010; Morigi et al. 2012; Schöttner et al. 2012). The biodiversity associated with these ecosystems is comparable to that found in tropical coral reefs (Roberts et al. 2006, 2009). Cold-water coral buildups occur in a variation of settings such as on continental slopes, seamounts, plateaus, ridges, and submerged sides of oceanic islands (Rogers 2004; Davies et al. 2008; Roberts et al. 2009; Wienberg and Titschack 2015).

Cold-water corals are associated with permanent or episodically strong currents, because the currents supply food and disperse eggs sperms and larvae, remove waste products and winnow the sediment thus avoiding the burial of corals (Rogers 2004). However, recent studies have indicated that removal of waste products and winnowing of sediment by currents seems are irrelevant aspects for cold-water coral growth (Larsson and Purser 2011; Purser and Thomsen 2012; Titschack et al. 2015). But the requirement for a strong current influences the distribution and growth form of corals at all scales (Rogers 2004; Davies et al. 2008). Cold-water corals are usually associated to food supply that is commonly driven by the interplay of surface water productivity, the bottom current regime (e.g., internal

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waves, internal tides, downwelling and cascading) and the topography of the bottom (Frederiksen et al. 1992; Reed 2002; Freiwald et al. 2004; Duineveld et al. 2004, 2007; White et al. 2005; Mienis et al. 2012; Hebbeln et al. 2014).

Cold-water corals were previously not reported from the Maldives or the northern Indian Ocean (Freiwald et al. 2004, 2005; Davies et al. 2008; Roberts et al. 2009). The aim of this study is to present the first record of fossil (upper Pleistocene) cold-water corals from the Maldives. This research is also focused on the analysis of the coral assemblage and the associated epibionts as a proxy for interpreting the paleoenvironmental conditions at the time of coral growth and to compare them with recent conditions. In addition, as a secondary objective, the analysis of epibiont assemblages allows interpreting the behavior of these organisms.

Geological setting

The Maldives archipelago in the central equatorial Indian Ocean is an isolated tropical carbonate platform constituting the central part of the Chagos-Laccadives Ridge, southwest of India (Fig. 1). A north–south-oriented double row

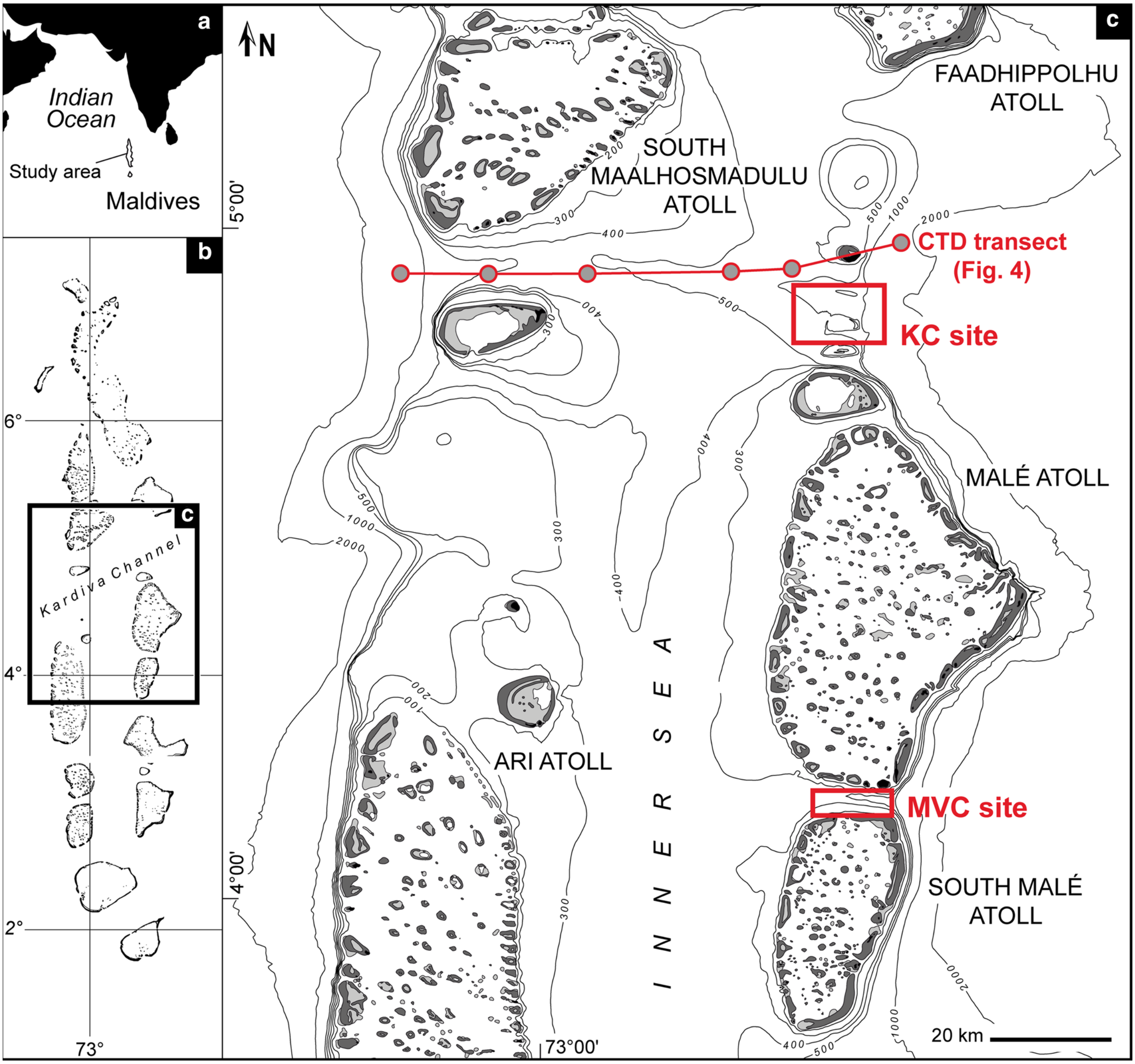

Fig. 1 Geographic location of the Maldives archipelago in the Indian Ocean (**a**, **b**) and **c** setting of the studied sites in the Kardiva Channel (KC) and Malé Vaadhoo Channel (MVC)

of atolls encloses the Inner Sea of the Maldives (Fig. 1). Atolls are separated from each other by inter-atoll channels, which deepen towards the Indian Ocean (Purdy and Bertram 1993). The Inner Sea is a bank-internal basin with water depths of up to 550 m. The Maldives carbonate sedimentary succession is almost 3 km thick; it accumulated since the Eocene, away from any terrigenous input (Aubert and Droxler 1992; Purdy and Bertram 1993; Betzler et al. 2009, 2013).

The archipelago comprises about 1200 smaller atolls. Discontinuous marginal rims formed by smaller atolls (faros) surround lagoons with water depths of up to 50–60 m. The oceanward margins of the Maldives archipelago are generally steeply inclined, with dips of 20°–30° down to 2000 m of water depth. On the Inner Sea side, stepped atoll slopes have the same dip angles, but reach down to water depths of only 550 m, where the gradient rapidly declines (Fürstenau et al. 2010). The Inner Sea is characterized by periplatform ooze deposition (Droxler et al. 1990; Malone et al. 1990), locally accumulated into sediment drift bodies (Betzler et al. 2009, 2013; Lüdmann et al. 2013). Passages separating the atolls formed through the partial demise of larger carbonate banks during the middle Miocene (Betzler et al. 2009, 2013, 2016).

The climate and oceanographic setting of the Maldives is dictated by the seasonally reversing Indian monsoon system (Tomczak and Godfrey 2003). Southwestern winds prevail during northern hemisphere summer (April–November) whereas northeastern winds prevail during winter (December–March). Winds generate ocean currents, which are directed westwards in the winter and eastwards in the summer. Interseasonally, a band of Indian Ocean Equatorial Westerlies establish, enforcing strong, eastward-flowing surface currents showing velocities of up to 1.3 m s^{-1}. Currents reach down to the seafloor (Lüdmann et al. 2013), especially in the inter-atoll passages where submarine dunes and moats occur (Betzler et al. 2009, 2013; Fig. 2a, b).

Materials and methods

The studied samples were recovered during RV SONNE Cruise SO236 in August 2014 (Betzler 2015). The bathymetry of the study area was recorded with the hull-mounted multibeam system Kongsberg EM120 using a nominal sonar frequency of 12 kHz with 191 beams per ping and an angular sector coverage of 120°–140° for most survey lines to suppress low quality signals from the outer range. Equidistant beam spacing was used for all lines. The software package Caris HIPS was used for onboard-processing and editing of the swath echosounder and navigational data. Surfaces with resolutions of 5, 10, and 30 m were created using the CUBE algorithms implemented in CARIS and exported as ESRI ArcGIS grid for visualization with IVS Fledermaus (Interactive Visualization Systems Inc.).

Sub-bottom profiles were recorded using the onboard parametric sediment echosounder Atlas PS70. The system operated with two frequencies (18 and 22 kHz) emitted in a 4° cone from two hull-mounted transducers. Data were stored in the Parasound-native format ps3 and the raw-data format ASD for processing. The ps3 data were converted with the tool ps3segy (Hanno Keil, University of Bremen, Germany) into the standard seismic data format SEG-Y. Processing was performed using the software ReflexW (Sandmeier Software) and comprises automatic gain control (AGC) and amplitude normalization along the profile.

Profiles of conductivity, potential temperature, salinity and dissolved oxygen were derived from calibrated CTD measurements along a W-E transect (Fig. 1c) using a Seabird 911 CTD Sonde mounted on a Seabird Carousel Sampler equipped with 24 10-l Niskin bottles to collect water samples. The different parameters were visualized with the Ocean Data View software package (Schlitzer 2015).

Sea floor sampling was performed with the RV Sonne video grab sampler (five samples) and a box corer (two samples). The video grab sampler also provided a visual record of the sea floor surface that allowed the identification of sedimentary features and cold-water coral distribution prior the sampling. The sediment samples were separated into distinct fractions (>2, >0.25, >0.063, and <0.063 mm) and described accordingly. Composition of coral assemblages was analyzed from 88 specimens from MVC and 112 specimens from KC. In addition, 22 thin-sections (ten from MVC and 12 from KC) were prepared for analyzing preservation of cold-water corals and the presence of microborings.

Sample preparation and measurement as well as correction for $^{13}C/^{12}C$ ratio and calculation of conventional radiocarbon ages (CRA) were performed by Beta Analytic Inc. (Miami, USA) on selected coral fragments. In order to avoid contamination of samples for dating by younger material, the encrusters as well as the surficial alteration crust on the corals were removed and areas affected by microborings were avoided. Samples were cleaned with ultrasounds in deionized water and were visually inspected for cements, overgrowths and fills. Calibration of conventional radiocarbon ages was done with the software Calib (v.7.0.4., Stuiver and Reimer 1993) using the calibration curve “MARINE13” (Reimer et al. 2013) and a global reservoir correction of 200–500 years to account for the delay in atmosphere–ocean exchange of ^{14}C. Calibrated ages (cal BP) are rounded to the next decade and provided as median of the probability distribution with 2σ error range (95.4% probability).

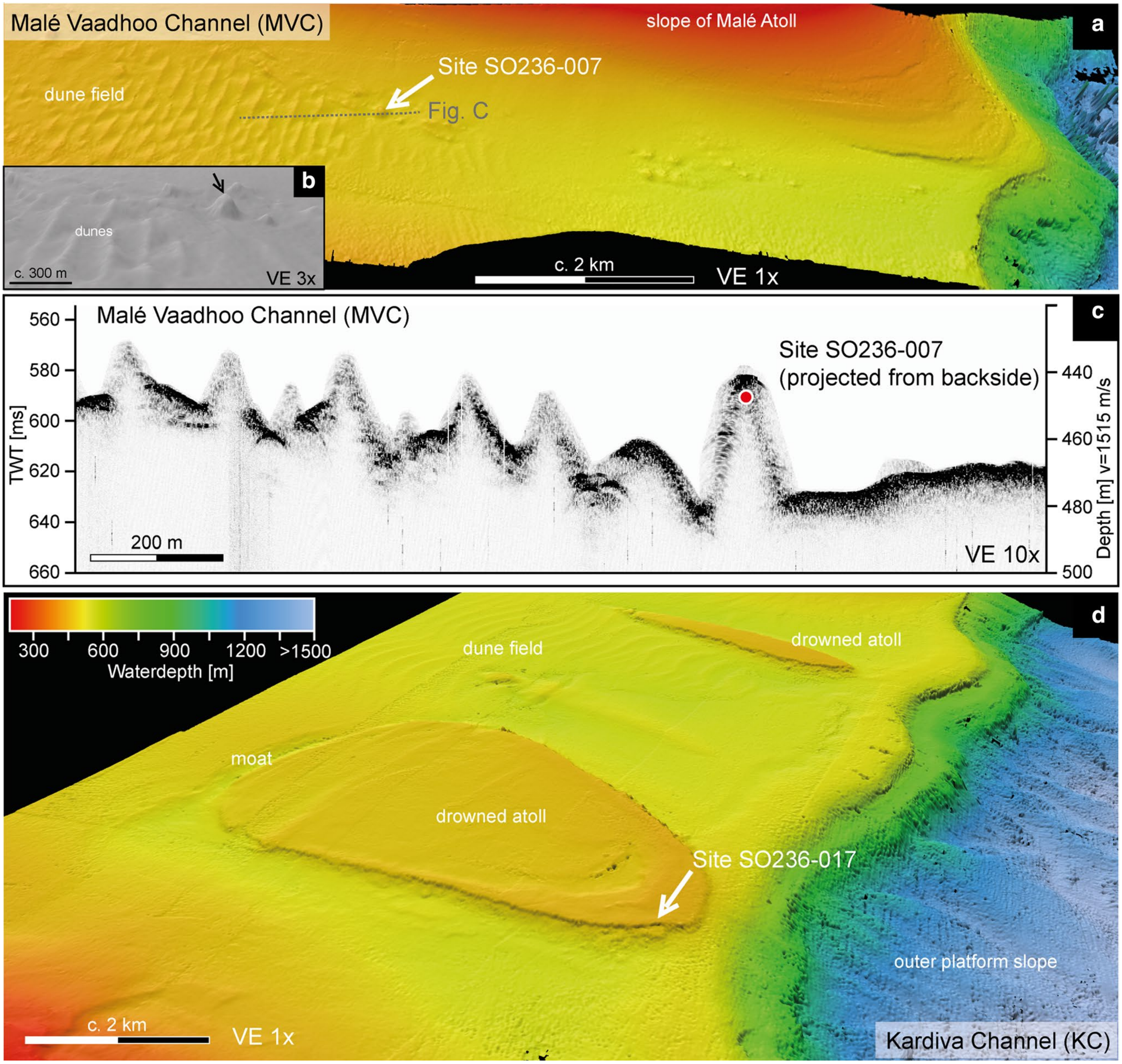

Fig. 2 Multibeam bathymetry. **a** Eastern Kardiva channel between atolls Gaafaru and Faadhippolhu (see Fig. 1 for location). **b** Malé Vaadhoo Channel (see Fig. 1 for location). **c** Backscatter image of the dune field and the submarine blocks of Malé Vaadhoo Channel. **d** Parasound profile of the dune field at Malé Vaadhoo Channel (Fig. 2b). *Red dot* shows the position of the cold-water coral accumulations at the top of a flank of the submarine block. *VE* vertical exaggeration

Epibionts and endobionts (borers and microborers) were analyzed on surface of cold-water corals and thin-sections under stereoscopic microscopy (Olympus SZ60, Universidad de Jaén). Epibiont relationships were studied on cold-water coral surfaces using the overgrowth ability index of Taylor (1979). This index was calculated for each microencruster using Taylor's formula:

$$\text{Overgrowth ability index} = \frac{(\text{Frequency as an overgrower}) \times 100}{(\text{Frequency as an overgrower} + \text{frequency overgrown})}.$$

This simple index expresses the number of successful overgrowths as a percentage of the total number of overgrowth interactions. Lateral and frontal overgrowths among microencrusters are not differentiated, because such structures can only be observed in thin-sections. The overgrowth ability index in this paper is treated as an approximation to the

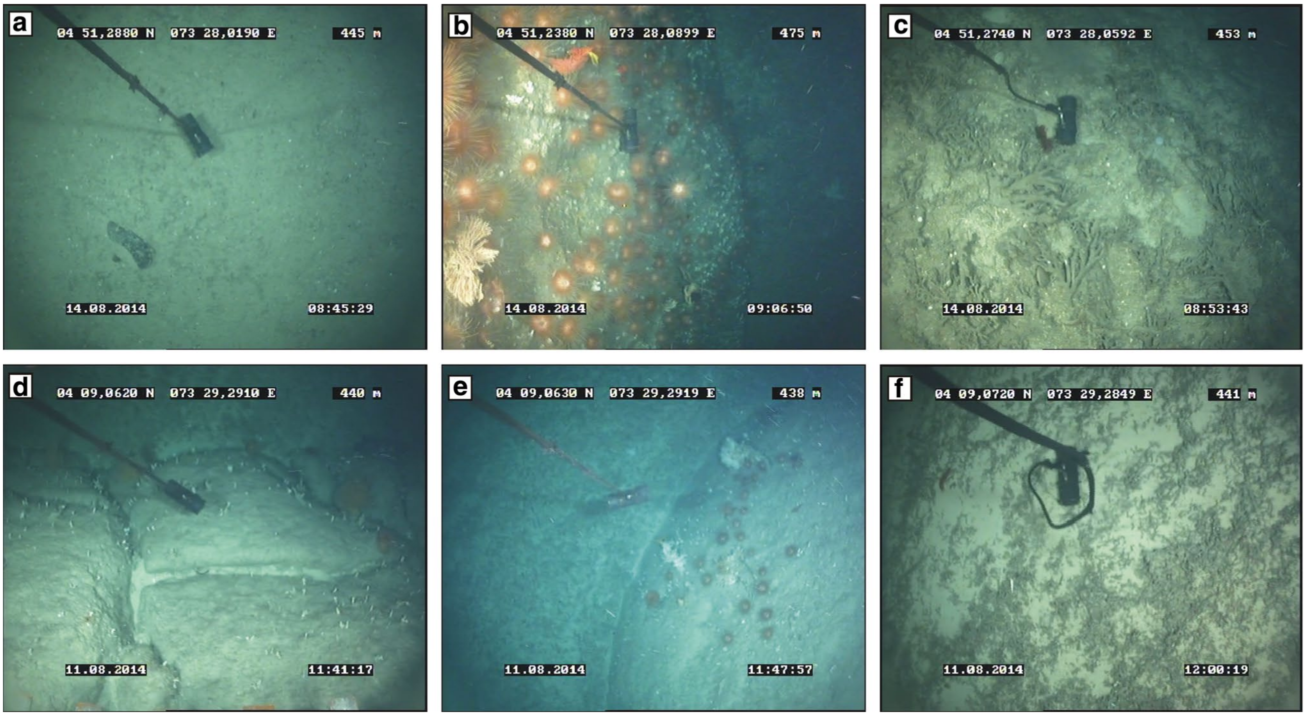

Fig. 3 Sea-floor images obtained by the TV Grab sampler. The *scale length* is 20 cm. **a** Rocky sea floor at the top of the drowned atoll at the eastern Kardiva channel. **b** Cliff separating two terraces of the drowned atoll at the eastern Kardiva channel. The cliff is nowadays colonized by echinoids, bryozoans, hydrozoans and crustaceans. The bottom of the cliff is in contact with the cold-water coral rubble (*right*). **c** Cold-water coral rubble at eastern Kardiva channel. *Enallopsammia* is dominant in this area and reaches up to 40 cm in size. **d** Subvertical wall of the large flank of the block at Malé Vaadhoo channel (Fig. 2d). The rock surface is colonized by robust branched bryozoan and with sediment pockets with cold-water coral rubble (*upper part of the picture*). **e** Contact between the cold-water coral rubble (*left*) and the submarine cliff rocky surface encrusted by echinoids, bryozoans and sponges (*right*). **f** Cold-water coral rubble with abundant *Lophelia* floating in a fine grained sediment matrix

true relationships among microencrusters, since overlapping is a complex three-dimensional phenomenon.

Results

Depositional and oceanographical setting

Cold-water corals were found at two stations at the eastern flank of the archipelago. SO236-007 to the south is located at 04°09,07′N, 73°29,28′E, and SO236-017 to the north at 04°51.26′N, 73°28.05′E (Figs. 1, 2).

The southern site is located between Malé Atoll and South Malé Atoll in the eastern part of the Malé Vaadhoo Channel (MVC, Figs. 1, 2b–d). Cold-water corals are recorded at a water depth ranging from 437 to 448 m. Samples were recovered from 443-m depth. The channel floor is covered by some blocks and a several kilometer wide field of submarine dunes at a water depth of 390 m (Fig. 2c, d). The submarine dune sediment consists of bioclast-rich carbonate sands with common skeletal remains >2 mm. The main components are bryozoans, bivalves (mainly pectinids), gastropods, *Halimeda* plates, pteropods, and benthic foraminifera. The occurrence of *Halimeda* and the benthic foraminifera *Amphistegina* indicates sediment export from the shallow-water areas of the faros lining the channel and reworking of the sediment by the bottom currents flowing in the channel. Adjacent to the dune field, there are several blocks, which are up to 40 m high. The block, where the cold-water coral samples were taken, is sediment barren (Fig. 3d) and consists of a moderately bedded and fractured carbonate rock colonized by abundant hydrozoans and echinoids on submarine cliffs (Fig. 3e). At the flanks of the block there are sediment pockets with autochthonous/para-autochthonous cold-water coral rubble (floatstone texture) with a fine-grained wackestone matrix (Fig. 3f) which is rich in bioclasts such as planktic and benthic foraminifera, mollusk fragments, pteropods, echinoid fragments, and sponge spicules. The cold-water corals act as baffles of fine sediment due the surrounding rocky ground, where sediment is winnowed.

The northern site is located at the eastern end of the Kardiva Channel (KC) between Gaafaru Atoll and Kaashidhoo Atoll at a water depth ranging from 453 to 457 m

(Figs. 1, 2a, 3a–c). The bottom presents a stepped topography with submarine cliffs. The coral samples were recovered at 457-m depth on the terrace between two submarine cliffs (at the foot of a 9 m submarine cliff and over a 28 m submarine cliff). These submarine cliffs are the wall of a drowned Miocene atoll (Betzler et al. 2009, 2013). The cliff consists of bedded and fractured bare rock and the surface of the rock is locally colonized by echinoids, bryozoans, serpulids, bivalves, sponges, and hydrozoans (Fig. 3b). The cold-water coral rubble is located on a terrace of the drowned atoll flank. The matrix among cold-water coral debris is an unconsolidated carbonate sediment with a poorly sorted floatstone with the debris of the biota associated with cold-water corals floating in a fine-grained wackestone texture with a periplatform ooze matrix. The cold-water corals are autochthonous (autochthonous). The surrounding bottom is a rocky ground where benthic organisms are scarce (Fig. 3a). The fine sediment is retained between cold-water corals meanwhile this sediment is winnowed from surrounding rocky ground.

The surveys with the video grab sampler shows that at both sites there are no living scleractinian corals (Fig. 3c, f). Radiocarbon dating results on the cold-water corals give a conventional radiocarbon age of 21,400–21,840 ± 60 BP for MVC and 22,190–22,540 ± 60 BP for KC (Table 1). The only living macrofauna colonizing the coral rubble is represented by *Gorgonia* and solitary corals.

The CTD profiles in the Kardiva Channel display strong and stable temperature stratification throughout the Inner Sea with a sharp thermocline at a water depth of 80–90 m (Fig. 4). Average temperatures in the surface mixed layer varied between 28 and 29 °C and plot well within the range of the climatological mean for August. Below the thermocline, at 500 m, temperatures decrease to about 12 °C (Fig. 4). Dissolved oxygen concentrations are around 4.03 ml/l in the upper mixed layer, sharply declining to 1.12–1.34 ml/l below the thermocline. A distinct oxygen minimum with concentrations of about 0.896 ml/l is observed around 500-m water depth. Salinity attains values of around 35.8 psu above the thermocline and averages 35.3 psu below; slightly higher values of 35.35 psu were recorded at the depth where the cold-water corals were found (Fig. 4). The values of neutral density, calculated from the salinity and temperature profiles, are lower than 23 kg/m^3 above the thermocline, gradually increasing to 27.25 kg/m^3 at the depth of the cold-water coral sampling site (Fig. 4).

Composition of coral assemblages

The coral assemblage is composed by representatives of the Order Scleractinia such as *Enallopsammia* (Family Dendrophylliidae), *Lophelia* and *Desmophyllum* (Family Caryophylliidae), *Madrepora* (Family Oculinidae) and *Stephanophilia* (Family Merulinidae) The Order Alcyonacea is represented by the genus *Gorgonia* (Family Gorgoniidae) (Fig. 5). Coral assemblages from both settings are dominated by *Lophelia pertusa* (88% at the MVC, 68% at the KC site; Fig. 6) followed by *Madrepora oculata* (8% at the MVC site and 20% at the KC site) and *Enallopsammia rostrata* (1% at the MVC site and 8% at the KC site). *Desmophyllum* and *Stephanophyllia* are only recorded at the MVC site (Fig. 6).

Preservation of corals

The corals are fragmented and the size of the fragments depends on the taxa. Mean size of *Lophelia* is 3.8 cm at the MVC site, and 3.2 cm at the KC site. The debris of the second most abundant genus *Madrepora* is 4.9 cm large in average at the MVC site and 4.2 cm at the KC site. The maximum size of *Lophelia* fragments is 11 cm the KC site and the maximum size of *Madrepora* pieces is 34 cm at the MVC site. The larger specimens of corals correspond to genera *Enallopsammia* (mean size 11.3 cm).

Coral fragments are characterized by distinct colors. At the KC site, *Enallopsammia* and some *Madrepora* mostly have a brown surficial phosphatic stain with Fe–Mn oxyhydroxides (see Freiwald et al. 1997; Freiwald and Wilson 1998). Such specimens are denser and do not have an inner porosity. The upper surface of *Enallopsammia* specimens are affected by corrasion (sensu Brett and Baird 1986) as well as abundant borings and microborings (Fig. 7a). The white specimens (*Lophelia* and *Madrepora*) are comparatively well preserved, without corrasion facets and low incidence of borings. Those are generally located in the theca, in the growth density bands of *Lophelia*. Growth density bands are poorly developed in *Madrepora*.

Corals from the MVC site are white, grey-light blue, and brown in color. Corrasion facets and borings are scarcer than in KC samples. Growth density bands are well developed, mainly in *Madrepora* specimens, where borings of sponges are located in the theca (Fig. 7b–f).

Description of epibiont communities

Malé Vaadhoo Channel

At the MVC site, the main epibionts on the corals are tube-dwelling encrusting serpulids dominated by *Spirorbis* (small spirally-coiled tubes) and *Serpula vermicularis*. *Filograna*, *Hydroides*, and *Placostegus* are less abundant (Figs. 8, 9). Other undifferentiated serpulids with a prominent keel have been included in the morphogroup dorsoserpula. The *Spirorbis* specimens are characterized by a sinistral coiling tube with a smooth porcellanous surface and

Table 1 The ^{14}C calibrated age of well-preserved cold-water corals from Malé Vaadhoo Channel (SO236-007-TVG) and Kardiva Channel (SO235-017-TVG and SO235-017-TVG-2)

Sample ID	Material	Coordinates		$^{12}C/^{13}C$	^{14}C age	Calibrated age (ΔR 0)				
		WGS84		o/oo	Year BP	Calibration curve	cal BP (2σ ranges, 95.4% probability)			
		Lat	Lon				Calibration curve	Range (years)	Rel. area u. distribution	Median of prob. (ky)
SO236-007-TVG	Coral	4°09.07′N	73°29.31′E	−4.6	18,250 ± 60	18,250 ± 60	MARINE13	21,400–21,840	1.00	21.63 ± 0.22
SO236-017-TVG	Coral	4°51.69′N	73°27.34′E	−6.4	18,920 ± 60	18,920 ± 60	MARINE13	22,250–22,540	1.00	22.40 ± 0.15
SO236-017-TVG-2	Coral	4°51.69′N	73°27.34′E	−7.2	18,900 ± 70	18,900 ± 70	MARINE13	22,190–22,540	1.00	22.38 ± 0.18

occasional faint growth rings. These forms are tentatively attributed to *Spirorbis corallinae*. Less frequent specimens of *Spirorbis* have sinistral tubes with three prominent longitudinal ridges but preservation impedes species determination. *Spirorbis* constitutes 79% of the epibionts, while the remaining serpulids constitute 19% (Fig. 8). The proportion of *Spirorbis* with respect to other epibionts is lower on *Lophelia* (73%) than on *Madrepora* (87%). Other epibionts such as bryozoans, bivalves, and barnacles are scarce (Fig. 8). Bryozoans are mainly recorded on *Madrepora* (2% of the epibionts). Bivalves and barnacles are exclusively recorded on *Lophelia* (always <1% of the epibionts). *Spirorbis* exclusively colonizes the external surface of the corals, whereas other serpulids are also located over the coral calice and within the calice between the septa in *Lophelia* specimens (e.g., *Filograna*, Fig. 9c). Serpulids located within the calice constitute aggregates of fine tubes. Bioerosion of growth density bands is well developed in *Madrepora*, where corallites are mainly bioeroded by boring sponge *Alectona millari* and clionaid sponges (Fig. 7). The boring sponges form networks of cavities which may eventually ramify. Fungal microborings are poorly recorded.

Kardiva channel

At the KC site, the assemblage of epibionts, which is mainly represented by encrusters, is more diverse than at the MVC site (Figs. 8, 10). It encompasses serpulids, bryozoans, benthic microbial mats, encrusting foraminifera, sponges, solitary corals, *Gorgonia* and terebellids, as well as abundant ophiuroids, ostracods, echinoids, gastropods, and brachiopods living between the coral branches (Figs. 10, 11).

The assemblage of epibionts strongly differs between the corals with the phosphatic crust (mainly *Enallopsammia* and scarce specimens of *Madrepora*) and the white corals (*Lophelia* and *Madrepora*). The brown corals are covered by a diverse assemblage of living encrusters (Fig. 11) dominated by bryozoans (30% uniserial morphotypes, 14% massive morphotypes) and siliceous sponges (23%). The rest of the assemblage is composed by encrusting agglutinated foraminifera (11%), *Gorgonia* (5%), ophiuroids (5%), encrusting calcitic foraminifera (4%), serpulids (3%), microbial mats (2%), solitary corals (2%) and barnacles (>1%). Among the sessile foraminifera, the arborescent dendrophryid form *Spiculidendron* with tubular branches is common and generally attached to the downward-oriented *Enallopsammia* surfaces. Siliceous sponges and microbial mats are commonly located between the coral branches just in the bifurcation. Moreover, sponges and ostracods are common in the calices of *Enallopsammia*.

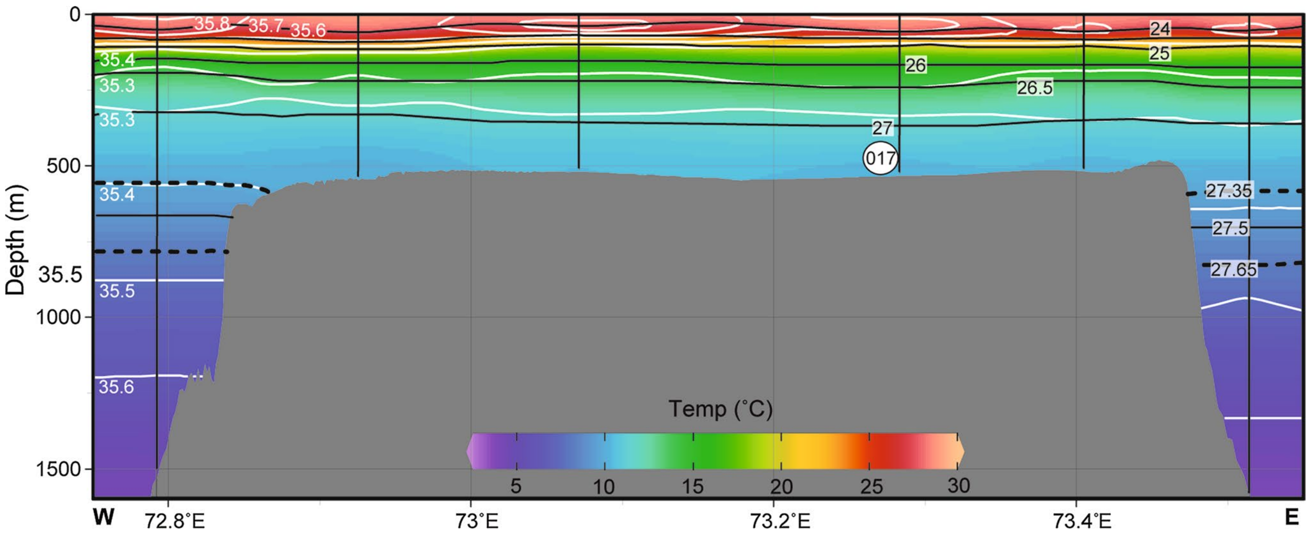

Fig. 4 CTD Profiles of temperature (°C) and salinity (psu, *white line*) of the water across the Kardiva channel. *Black dashed lines* represent the neutral density range (kg/m^3) in which cold-water corals can develop (Dullo et al. 2008). Position of CTD stations is shown in Fig. 1

The assemblage of epibionts on white corals is composed mainly of dead organisms and is dominated by serpulids such as *Spirorbis* (74% on *Madrepora* and 71% on *Lophelia*; Fig. 10j, k) and other serpulids (20% on *Lophelia* and 5% on *Madrepora*). Uniserial encrusting bryozoans (12% on *Madrepora* and 3% on *Lophelia*) and massive encrusting bryozoans (6% on *Madrepora* and 5% on *Lophelia*) are very diverse. Less common encrusters are siliceous sponges and terebellids.

In addition to epibionts, an endolith assemblage is recorded composed by clionaid sponges (*Entobia* ispp.) and fungi (*Orthogonum* ispp.).

Overgrowth interactions between epibionts

Spirorbis is mainly encrusted by other *Spirorbis* (63%) and secondarily by other serpulids, sponges, and balanids ($n = 45$). The main epibionts on the other serpulids are *Spirorbis* (61%) and other serpulids, microbial mats (30%), and minor bryozoans, sponges, sessile foraminifera and balanids ($n = 57$). Massive encrusting bryozoans are mainly overgrown by *Spirorbis* (36%) uniserial bryozoans (21%), and a minority by other serpulids, siliceous sponges, solitary corals and sessile foraminifera ($n = 15$). Recent microbial mats are only encrusted by agglutinated encrusting foraminifera. Recent sponges related to the coral remains are very small (usually <3 cm diameter) and scarcely encrusted by small serpulids and sessile foraminifera. However, recent sponges overgrow to recent massive bryozoans and recent solitary corals. The analysis of the overgrowth ability index (Taylor 1979) on Upper Pleistocene epibionts (not recent living specimens) shows higher values for sessile foraminifera (100%), *Spirorbis* (85%) and uniserial bryozoans (83%), meanwhile lower ones correspond to recent solitary corals (33%), large serpulids (29%) and massive bryozoans (12%).

Discussion

Environmental requirements

The controlling parameters of cold-water coral are current dynamics, temperature, water density, vertical and bed-load sediment supply, oxygenation, pH, and the most important, food supply (Freiwald et al. 2004; White et al. 2005; Duineveld et al. 2007; Roberts et al. 2009; Wienberg et al. 2010; Eisele et al. 2011; Fink et al. 2012, 2013; Mienis et al. 2012; Flögel et al. 2014; Hebbeln et al. 2014). Cold-water corals live in aphotic waters by preying mainly on zooplankton that drifts past the coral framework, especially in zones with bottom currents (however, at least for *L. pertusa*, other food sources have been mentioned; see Duineveld et al. 2007, 2012; Dodds et al. 2009; Tsounis et al. 2010). Moreover, they require a hard substrate on which to attach.

Lophelia pertusa has a nearly cosmopolitan distribution in water with temperatures between 4 and 13.9 °C (Roberts et al. 2006; Freiwald et al. 2009), salinities of 31.7–38.8 psu (Freiwald et al. 2004; Davies et al. 2008) and dissolved oxygen contents lying between 2.7 and 7.2 ml/l (Dodds et al. 2007; Davies et al. 2008, 2010). *L. pertusa* has been recorded from water depths ranging from 39 to 2775 m (Roberts et al. 2009), and forming buildups between

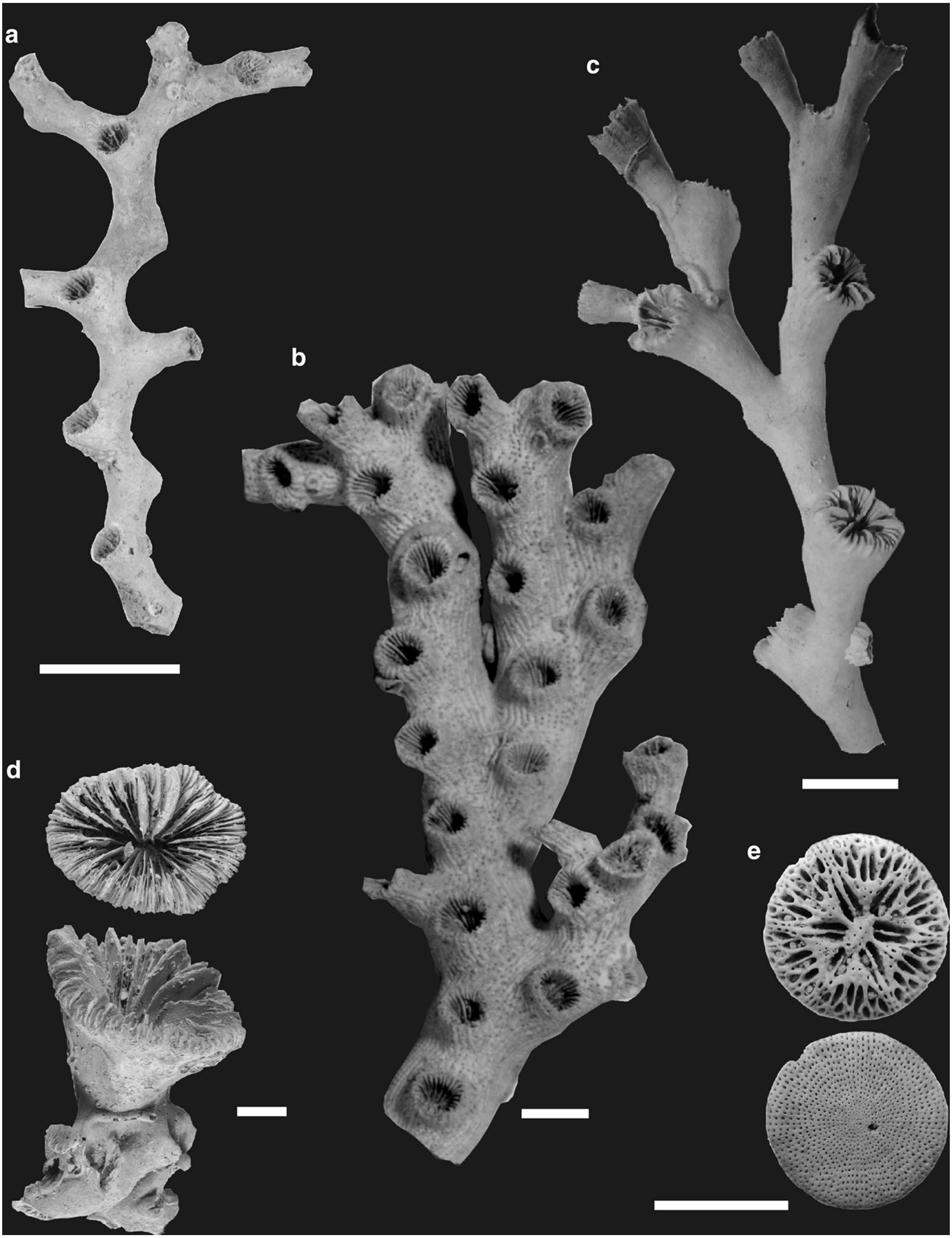

Fig. 5 Cold-water coral genera recovered from the two sampling sites. **a** *Madrepora.* **b** *Enallopsammia*. **c** *Lophelia* **d** *Desmophyllum*. **e** *Stephanophillia*

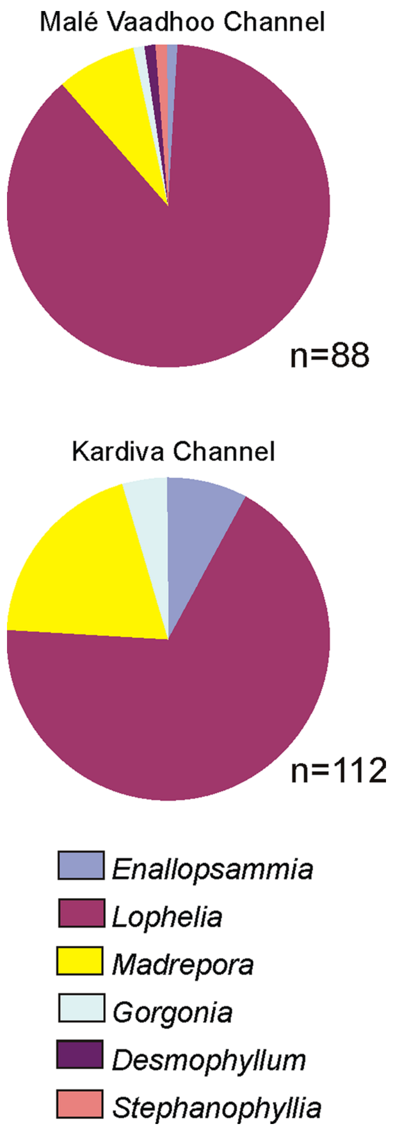

Fig. 6 Composition of fossil cold-water coral assemblages from Malè Vaadhoo Channel and Kardiva Channel

200- and 1000-m water depth (Davies and Guinotte 2011; Hebbeln et al. 2014).

Madrepora oculata is a secondary framework builder that occurs among colonies of *L. pertusa*. It is the most widespread cold-water coral taxa extending from 69°N off Norway to 59°S latitude in the Drake Passage (Hourigan et al. 2007) with a depth range from 55 to 1950 m (Zibrowius 1980). Colony branches have distinctive zigzag morphology.

The *Enallopsammia rostrata* specimens recovered in the samples form dendroid colonies that usually display an open-spaced growth habit with polyps in branches pointing in the same direction. *E. profunda* was reported as endemic to the western Atlantic (from Antilles to Massachusetts) at water depths of 145–1750 m (Cairns 1979; Hebbeln et al. 2014), and *E. rostrata* has been reported from the Atlantic, the Indian, and the western Pacific Ocean (Cairns et al. 1999) in depths from 215 to 2165 m (Cairns 1979).

The two studied cold-water coral occurrences in the Maldives are located at the Indian Ocean facing entrances of the inter-atoll seaways connecting the Inner Sea with the open Indian Ocean. The video surveys and the hydroacoustic data show that these areas are current-swept rocky bottoms as a flow of water is funneled through the straits as indicated by submarine dunes at the Inner Sea facing parts of the channels (Fig. 2; Betzler et al. 2009, 2013; Lüdmann et al. 2013). Therefore, one of the main pre-requisite for deep sea cold-water coral growth, the formation of a current-swept substrate with no or little sedimentation, is fulfilled.

Cold-water corals feed on fresh phytodetritus, zooplankton or on a combination of both (Duineveld et al. 2004, 2007; Kiriakoulakis et al. 2005; Becker et al. 2009; Carlier et al. 2009; Dodds et al. 2009). The locations of the cold-water coral sites in seaways near the edge of the carbonate archipelago are favorable for a constant flow of water providing food to the cold-water corals.

According to Rogers (2004), cold-water corals also tend to live in areas with stable physical conditions and limited annual variations in temperature and salinity. Cold-water corals are often associated with the most salty water mass at a depth that often coincides with the oxygen minimum zone (Freiwald et al. 2002; Rogers 2004) where bacterial activity related to the nutricline is high. Kenyon et al. (2003) suggested that cold-water coral buildups in the North Atlantic are related to the oxygen minimum zone, that usually corresponds with high dissolved inorganic carbon and pCO_2, because the oxygen minimum zone arises from remineralization of organic matter and therefore consumption of oxygen and release of CO_2 (e.g., Findlay et al. 2014).

The water temperature is a further factor controlling the occurrence of cold-water corals (Roberts et al. 2009). For example *L. pertusa* is exclusively present at water temperatures between 4 and 13.9 °C (Roberts et al. 2006; Freiwald et al. 2009). However, cold-water corals have been reported from extreme environmental conditions in the Cape Lookout area (NW Atlantic) where is the largest temperature variability (>9 °C in a day) measured in a cold-water coral habitat (Mienis et al. 2014). Water temperature at the depth of cold-water corals at the KC site is approximately 12 °C, and this value is within the normal range of *L. pertusa* occurrence. Salinity values of around 35.3–35.4 psu at the depth where the cold-water corals were found are within the 31.7–38.8 psu salinity range for dominant *L. pertusa,* according to Freiwald et al. (2004) and Davies et al. (2008). Therefore, temperature and salinity are within the range of

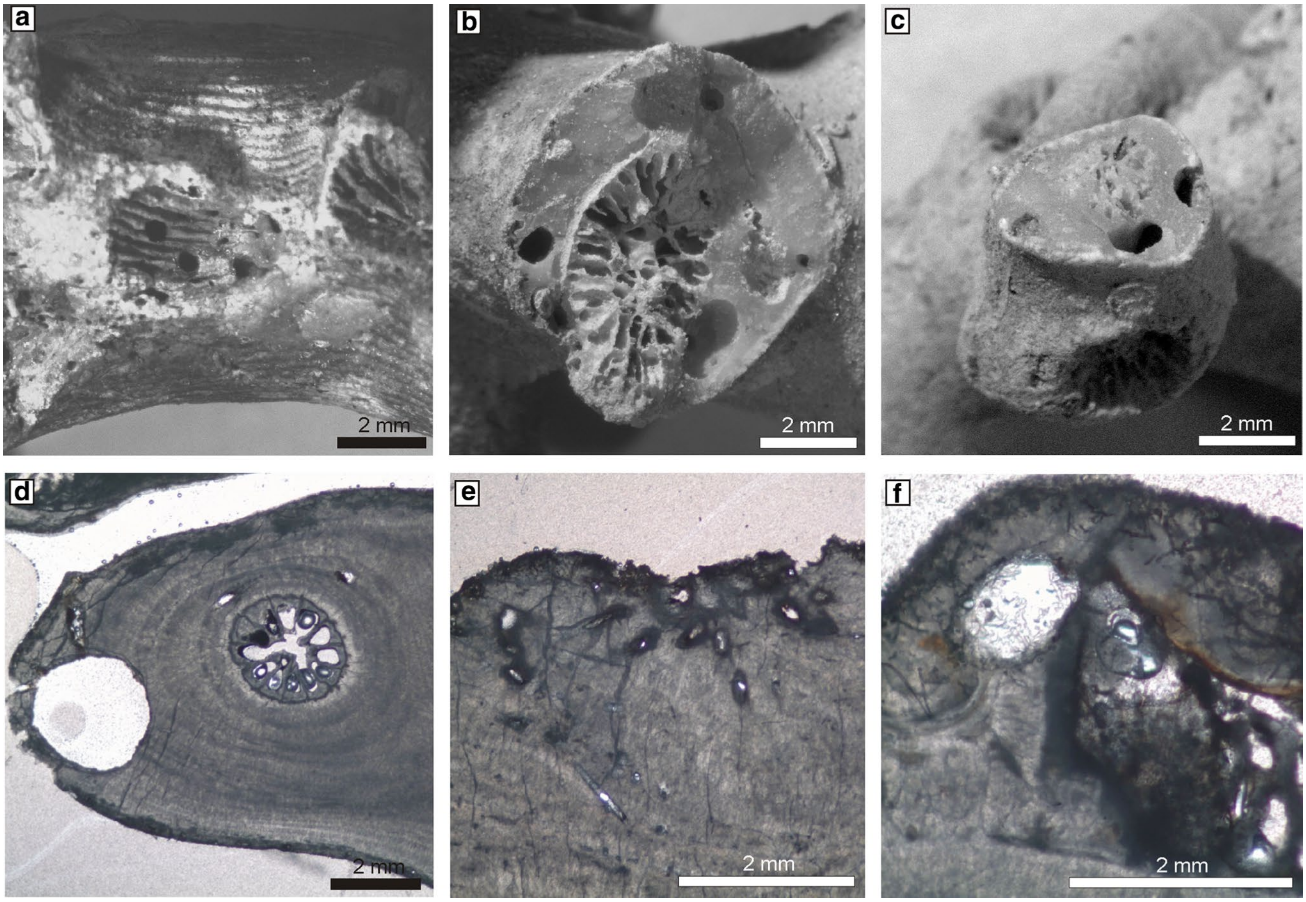

Fig. 7 Borings and microborings: **a** Microborings on an *Enallopsammia* specimen (*KC*). **b** Presence of large sponge chambers on growth density bands of *Lophelia* (*KC*) **c** Presence of large sponge chambers on growth density bands of *Madrepora* (*MVC*). **d** Thin section view of sponge chambers on growth density bands of *Madrepora* (*MVC*). **e** Microborings of fungi on *Enallopsammia* (*KC*) in thin section. **f** Microboring of fungi and boring of sponge on *Madrepora* in thin section (*MVC*)

cold-water corals and they are not the reason for explaining the absence of living cold-water corals.

Here, it is proposed the present-day oxygen and density conditions at the sampling sites are the factors which inhibit modern cold-water coral growth. Dissolved oxygen concentrations are around 0.896 ml/l at 500-m depth (Fig. 4), that is a sensibly lower value than the minimum oxygen conditions needed for *L. pertusa* to survive (>2 ml/l; Dodds et al. 2007; Davies et al. 2008, 2010; Brooke and Ross 2014). Cold-water coral reefs are reported to exclusively occur at certain density ranges, specifically from 27.35 to 27.65 kg/m^3 (Dullo et al. 2008), or even 27.38–27.61 kg/m^3 (Flögel et al. 2014). This narrow range is closely linked to the aragonite saturation state, which within this density range is easily incorporated to cold-water coral skeletons (Findlay et al. 2014). At the Maldives studied sites, the values of neutral density of around 27.25 kg/m^3 at the depth of cold-water coral occurrence are therefore out of the density envelope required for the cold-water coral to live according to Dullo et al. (2008) and Flögel et al. (2014).

Between 21.4 and 22.5 ka BP the global sea level was around 120 m lower than today (Lambeck and Chappell 2001) and therefore the different oxygen and density zones of the water masses with favorable conditions for cold-water corals occurred at the sea floor just at the location of KC and MVC areas where the cold-water coral rubbles are recorded today (these setting during the glacial lowstand of sea level were around 340-m depth for KC and 320-m depth for MVC). According to Tomczak and Godfrey (2003) seasonal and interseasonal currents in the monsoonal controlled area of the Indian Ocean reach water depths of 200 m and more with only slightly reduced velocities, which in the case of the Maldives is reflected by the formation of submarine dunes (Fig. 2) and drift bodies. Therefore, in a context of sea-level lowstand, the Malé Vaadhoo Channel and the Kardiva Channel were probably within favorable oxygen and density values and in a more favorable position with regard to the current regimes supplying the food supply to the cold-water corals. However, changes in other parameters such as changes in

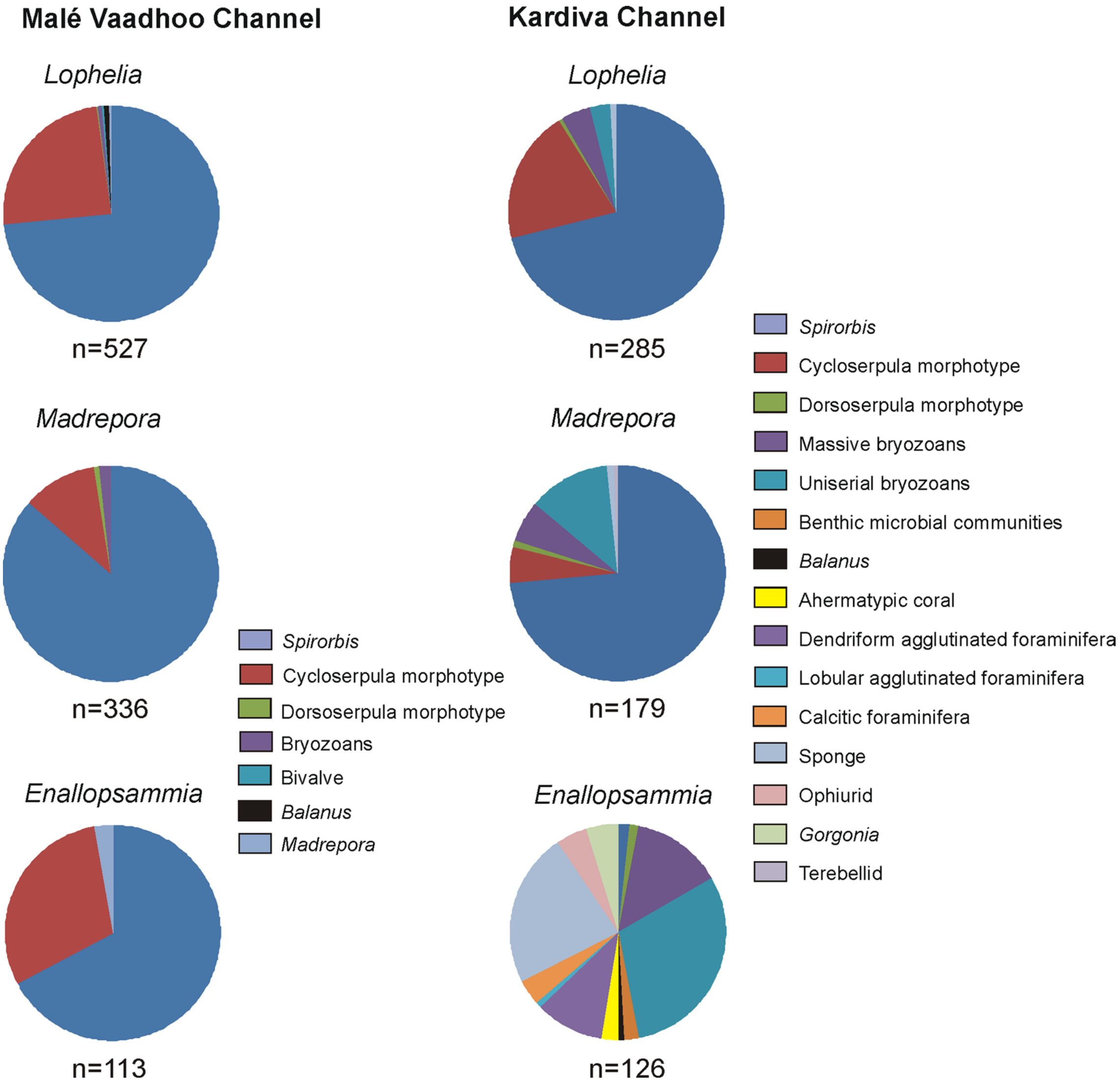

Fig. 8 Composition of epibiont assemblages from Malé Vaadhoo Channel and Kardiva Channel according to colonized cold-water coral genus

sedimentation rate, productivity in shallow waters (affecting to organic matter accumulation in the bottom and oxygenation) among others, related to sea-level lowstand conditions, are not considered as this cannot be resolved with the available data. More studies are needed in the future to elucidate these aspects.

Diversity of corals and epibionts

The benthic assemblage thriving in the Kardiva Channel is more diverse than the benthic assemblage from the Malé Vaadhoo Channel, both with regard to the corals and to the epibionts which are dominated by encrusters. The encrustation density of the corals is also higher in KC than in MVC. In addition, at the KC site the record of living encrusters (bryozoans, sponges, foraminifera, *Gorgonia*, solitary corals, balanids, dorsoserpula and microbial mats) and other epibionts (brachiopods, ostracods, and ophiuroids) is high. From MVC site, living specimens are less common, and they are restricted to bryozoans, sponges and *Gorgonia*, and rare cases of brachiopods, solitary corals and *Terebella.*

One factor which is proposed to control these differences is the sedimentation rate. Longer time of exposure of the coral substrate favors the colonization of bioclasts by epibionts including encrusters and borers and enforces the effect of corrasion (Jensen and Frederiksen 1992; Reolid and Gaillard 2007; Reolid et al. 2007). Especially the development of complex epibiont assemblages calls for a low rate of sedimentation (e.g., Jensen and Frederiksen 1992; Leinfelder et al. 1994). Sessile epibionts recorded at both sites from the Maldives are mainly

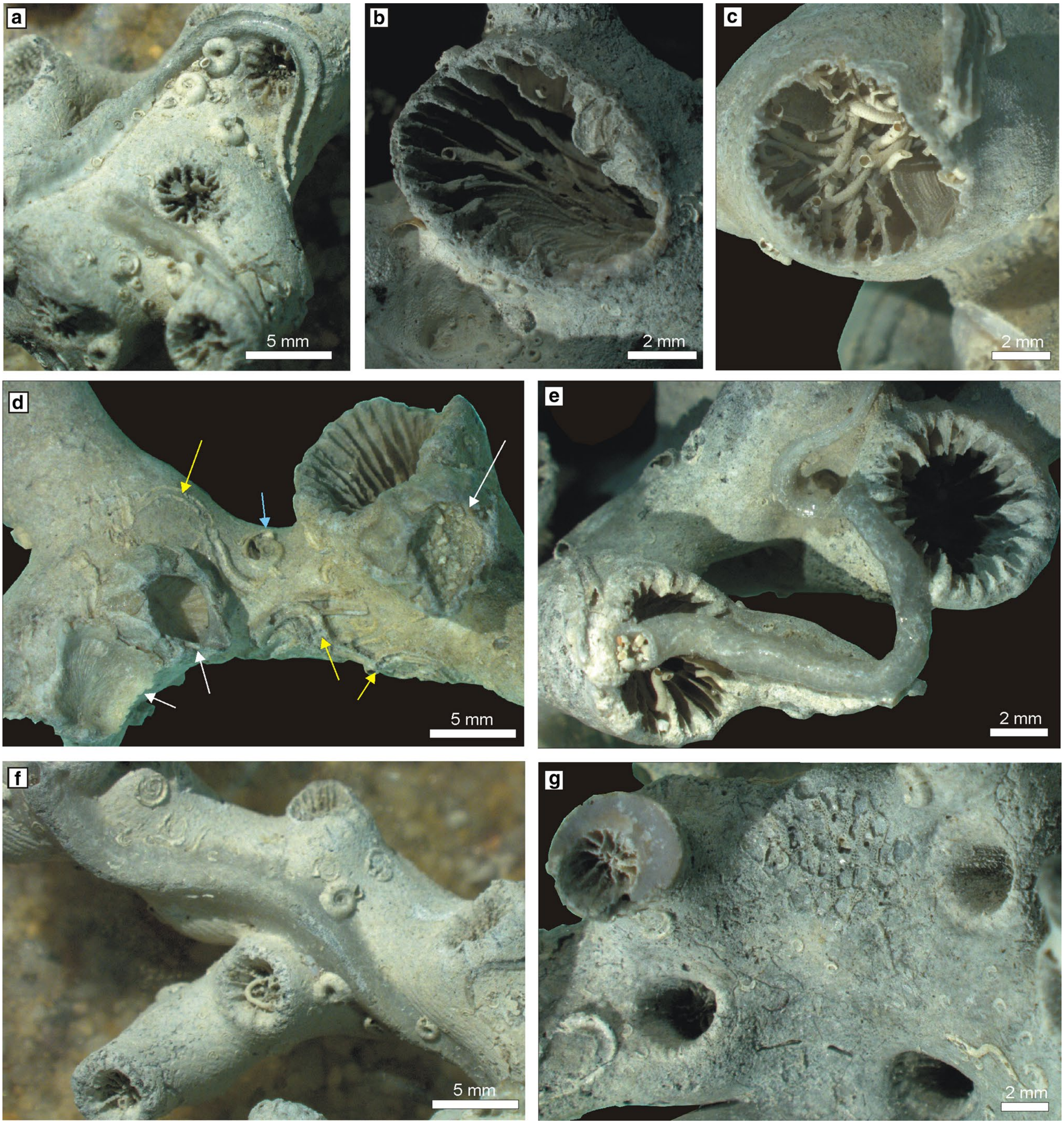

Fig. 9 Encrusters from cold-water corals of Malé Vaadhoo Channel. **a** Colonization of *Madrepora* by *Spirorbis* and serpulids. **b**, **c** Colonization within the calices of *Lophelia* by *Filograna*. **d** Presence of *Spirorbis* (*blue arrow*), serpulids (*yellow arrows*) and balanids (*white arrows*) on *Lophelia*. **e** Serpulid on calices of *Lophelia*. **f** *Spirorbis* encrusting *Madrepora* and large serpulid. **g** Bryozoans encrusting *Madrepora* surface

suspension-feeders and therefore are very sensitive to any influx of fine-grained sediments (Leinfelder et al. 1994; Reolid et al. 2005). Low sedimentation rates and low terrigenous input would be well indicated by the most diverse encruster assemblages and by high abundances of encrusters per surface. Other potential controlling factor on epibionts is the availability of food resources (see Gil et al. 2006; Leite et al. 2016).

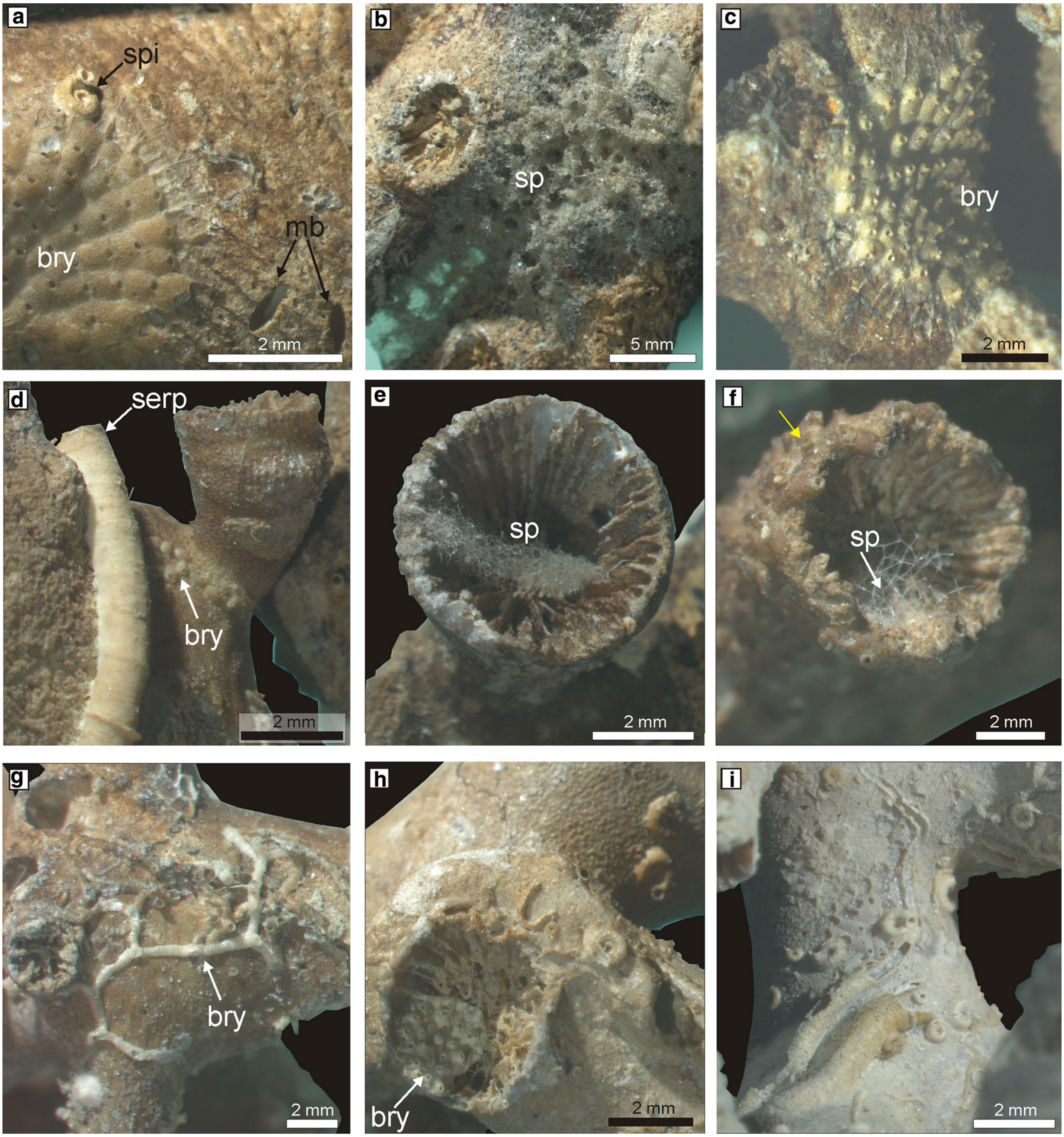

Fig. 10 Encrusters from cold-water corals of Kardiva Channel. **a** *Spirorbis* (spi), bryozoan (bry) and microborings (mb) from *Enallopsammia*. **b** Siliceous sponge (sp) encrusting *Enallopsammia*. **c** Massive bryozoans encrusting *Enallopsammia* specimen. **d** Serpulid (serp), bryozoans (bry) and solitary coral encrusting *Lophelia*. **e** Siliceous sponge (sp) within calice of *Lophelia*. **f** Calice of *Lophelia* colonized by siliceous sponge (sp) and bryozoans (*yellow arrow*). **g** Living uniserial bryozoans encrusting *Lophelia* surface. **h** Massive bryozoan (bry) encrusting calice of *Lophelia*. **i** Serpulids, *Spirorbis* and bryozoans encrusting *Madrepora*

Phases of colonization

The corals were colonized, both, during the lifetime and after death. Beuck et al. (2007) and Freiwald and Wilson (1998) indicate that thin soft tissue cover the external surface of juvenile corallites or the distal part of the adult ones, and protect against epibionts, whereas tissue-barren skeletal parts are infested by microborers and encrusters. In a

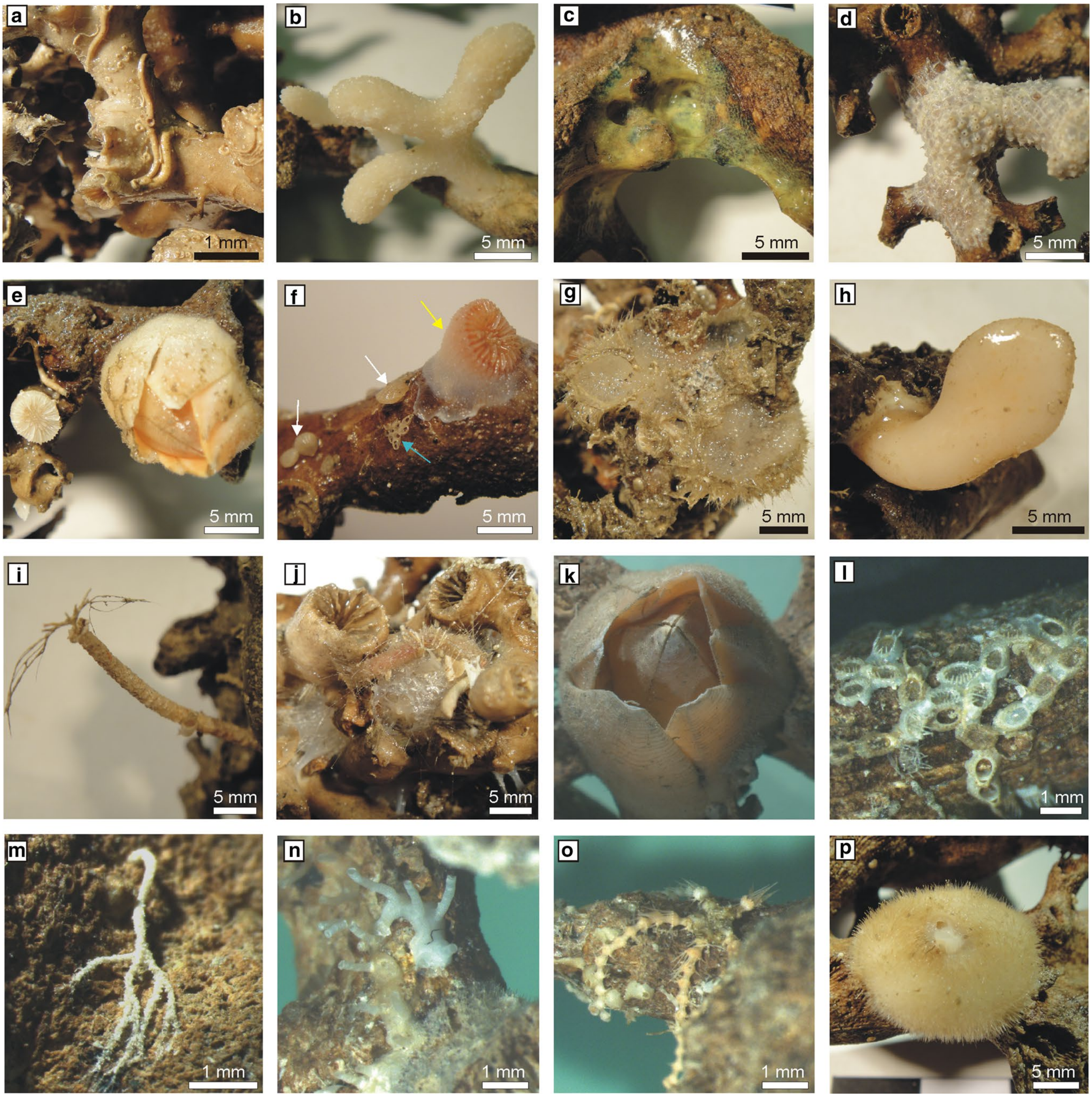

Fig. 11 Encrusters from cold-water corals. **a** Serpulids and *Spirobis* colonizing *Lophelia* specimen from KC. **b** Living *Gorgonia* attached to *Enallopsammia* from KC. **c** Living microbial biofilm growing on *Enallopsammia* from KC. **d** Living massive bryozoans encrusting *Lophelia* from KC. **e** Living balanid and solitary coral growing on *Lophelia* from KC. **f** Living specimens of solitary stony coral (*yellow arrow*, probably a Caryophylliidae), brachiopods (*white arrows*) and bryozoans (*blue arrows*) attached to *Lophelia* from MVC. **g** Living siliceous sponges between *Lophelia* branches from MVC. **h** Living indeterminate organism growing on *Lophelia* from MVC. **i** Indeterminate agglutinated foraminifera (astrorhizoid) attached to *Lophelia* from MVC. **j** Living siliceous sponges growing between *Lophelia* branches from MVC. **k** Living balanid attached to *Enallopsammia* from KC. **l** Recent uniserial bryozoans colonizing *Enallopsammia* from KC. **m** Dendrophryid form *Spiculidendron* (foraminifera) attached to *Enallopsammia* downward surface from KC. **n** Living specimens of uniserial tubular bryozoans growing between branches of *Enallopsammia* from KC. **o** Small ophiuroid living on *Enallopsammia* branches from KC. **p** Indeterminate sponge living on *Enallopsammia* from KC

healthy colony, coral is able to encrust repetitively attached epibionts by selectively secreted sclerenchyme layers (Freiwald et al. 1997; Freiwald and Wilson 1998) resulting in a thickening of the skeleton. According to Rosso et al. (2010) and Sanfilippo et al. (2013), serpulids copiously encrust dead colonies of corals and fragments, or tissue-barren branches of living colonies. Freiwald et al. (1997) indicates that skeletal areas which lack a mucus and epithelial tissue protection get rapidly colonized by other sessile invertebrates such as spirorbids and encrusting bryozoans. Therefore a substantial amount of *Spirorbis* colonization may have occurred on the coral branches during live. Available data, however, do not allow excluding the colonization of death corals and fragments by *Spirorbis*.

Some bryozoans and serpulids (*Filograna*) occur within calices of the corals, where they are found shelter between the septa. This is not compatible with the colonization of the polyps during lifetime. Some epibionts from the KC site were alive when sampled coming mainly from brown coral remains. These were siliceous sponges, microbial mats, solitary corals, *Gorgonia*, bryozoans, brachiopods, ophiurids, and scarce serpulids other than *Spirorbis*. Living specimens were more common at the KC site and very scarce at the MVC site.

Several corals, especially *Enallopsammia* from the KC site, were colonized by microborers previously to the encrustation by epibionts. According to Beuck et al. (2007), in adult corallites the lower part of the polyp can be slightly infested due the retraction of the soft tissue that protects against bioeroding organisms. Early postmortem alteration in *Lophelia* colonies is indicated by the formation of a biofilm (sometimes phosphatic of Fe–Mn oxy-hydroxides) and fungi infestation as reported by Freiwald and Wilson (1998) from *Lophelia* reefs from Sula Ridge (Mid-Norwegian Shelf). Rapid rates of microbial activity have also been measured from experiments in carbonate substrates in shallow waters, with initial phases of microendolithic organism infestation occurring during the first week, and intense colonization occurring after a few months (Perkins and Tsentas 1976; Kobluk and Risk 1977; Bromley et al. 1990; Chazottes et al. 1995; Wisshak 2006; Wisshak et al. 2010). Diversity and infestation rates of microborers decreases according to depth (light availability) (Vogel et al. 1999; Wisshak et al. 2005a) but hydrographic parameters (such as current velocities) and proximity of cold-water corals favored the diversity and progress of bioerosion (Mortensen et al. 1995; Wisshak et al. 2005a). Endolith assemblage is dominated by boring sponges such as *Alectona* and clionaids, and fungi. According to Freiwald et al. (1997) and Freiwald and Wilson (1998) fungi and bacteria infestation occurs before clionaid sponges. This assemblage is exclusively of heterotroph organisms and it is regarded as indicative of fossil and Recent open marine aphotic environments (Beuck and Freiwald 2005; Bromley 2005; Wisshak et al. 2005b). Cases of encrustation in previously microbored surfaces, mostly of *Enallopsammia,* are common, mainly in the brown specimens of the KC site, but epibionts affected by microboring were not observed. Thus, an initial phase of microboring activity could be halted by later colonization by encrusting organisms. Accordingly, the time for settlement was longer for encrusters than for microborers. After colonization and under favorable environmental conditions, encruster growth could be very rapid. For example, the growth rate of serpulids in shallow-marine environments reaches up to 75 mm/year (Simon-Papyn 1965).

Competition for substrate

An interpretation of spatial relationships of the settlement is complicated by the possibility that interacting organisms did not live contemporaneously (Palmer and Palmer 1977; Taylor 1979). As the age of these corals ranges between 21,400 and 22,500 BP, a long exposure time of the coral remains can be assumed and consequently a lower probability of a contemporaneous interaction between epibionts. Some living specimens were recovered with the RV Sonne video grab sampler and box corer and the relationships between these epibionts suggest that active competition for substrate space occur. However, most of the epibionts are empty carcasses with color and fragmentations indicating they were death long time ago. For example, not living specimens of *Spirorbis* are settled on fragmented tubes of the morphotype dorsoserpula. For these cases, interpretations of spatial and paleoecological relationships among epibionts are hard to perform.

In general, it is assumed that competitively superior microencrusters overgrow the skeletons of less adept competitors, although in some cases, fossilized overgrowths may result from encrustation over an already dead organism (Lescinsky 1997). The lower values of the overgrowth ability index of the massive encrusting bryozoans (13%) can be the result of: (1) a lesser ability of massive encrusting bryozoans than sessile foraminifera, *Spirorbis* or uniserial bryozoans to compete for the available substrate. Massive encrusting bryozoans would be pioneer organisms colonizing the substrate, including during life of corals. Then, more specialized encrusters would appear; (2) the colonization of massive bryozoans by other organisms occurs when the bryozoans were dead. Colonization of living massive bryozoans by other organisms impeded the metabolic processes and asphyxia the bryozoans. Elsewhere, bryozoans were interpreted as poor space competitors (McKinney and Jackson 1989; Nebelsick 1992).

Preferential colonization

The differential colonization is recorded in the analyzed Pleistocene cold-water coral assemblages. Changes in the composition of encrusters assemblages are identified in both settings depending on the infested coral genus. This selective colonization has been also described in the literature for recent sponges from Mediterranean (Koukouras et al. 1985, 1996). The differences in the proportions of encrusters as well as differences in diversity are stronger in the Kardiva channel.

The preferences of colonization are related to the location of the different encrusters in the coral specimens. Filkorn (1994) indicated that certain species of bryozoa encrusting *Madrepora* from James Ross Basin (Antarctica) preferentially encrust the upcurrent sides of coral branches. *Spirorbis*, large serpulids and massive bryozoans among others exclusively grow on the external surface of the corals, but small serpulids (cycloserpulids) are preferently located within the calice between the septa (e.g., in *Lophelia* from MVC, Fig. 8b, c). Sponges are commonly recorded within the calices of *Enallopsammia* from KC samples or between the coral branches just in the bifurcation. Because light is not a controlling parameter in the analyzed deposits, this preferential location in protected, less exposed parts responds to a cryptobiontic behavior for larvae fixation. This cryptobiontic distribution might be aimed to avoid predation, with a preferential location of small sessile animals on sheltered parts of available substrates, where larvae are protected. Vagile organisms recorded at the KC site, such as small specimens of ophiurids, are probably juvenile specimens which obtain trophic resources and protection within the coral branches. Thus, these cold-water coral patches are places where the benthic life, mainly sessile, is concentrated, which is clearly scarce off-rubble patches.

Jensen and Frederiksen (1992) indicate the role of random colonization by epibionts on deep-water corals as an additional factor for explaining the distribution of epibionts.

Conclusions

This is the first record of cold-water corals from the Maldives archipelago, where such forms thrived during the last glacial maximum, at least from 21,400 to 22,500 BP. Coral assemblages are composed mainly of *Lophelia*, followed by *Madrepora* and *Enallopsammia*. However, the composition and state of preservation varies between the sampling points in the Kardiva Channel and the Malé Vadhoo Channel. The cold-water corals grew at the eastern mouths of the inter-atoll channels during the Late Pleistocene when these settings presented favorable conditions for developing cold-water coral such as enhanced currents, higher oxygen values, and different density conditions. It is proposed that low oxygen and density conditions are the main restricting factors suppressing cold-water corals in the recent.

The epibiont assemblages are very diverse and abundant, and show different abundances between both studied sites as well as differences with regard to the colonized coral genus. Some living benthic organisms such as brachiopods, bivalves, gastropods, barnacles and ophiurids find refuge among coral branches actually and they are not observed in surrounding rocky ground. However, *Spirorbis*, the most common encruster reported on Kardiva Channel and the Malé Vaadhoo Channel sites is not recorded as living specimens. Environmental requirements of this group were probably similar to those of cold-water corals.

From our data and observations we deduce a series of general conclusions. (A) although the corals are dead, the coral debris still serves as a cradle for other species; (B) a tentative sequence of colonization is proposed with borers and *Spirorbis* being the first colonizers followed by other serpulids and bryozoans; (C) epibionts appear to select the coral genus or species to be colonized; (D) cryptobiontic life style of most of the epibionts is not related to photophobic behavior.

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