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Deep-sea ecosystem tipping points

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1. Introduction

Framework-forming scleractinian cold-water corals (CWC) are ecosystem engineers that form the base for biodiversity hotspots being widely distributed in water depths between 200 m and 1,000 m in the Atlantic Ocean (Roberts et al., 2009). CWC reefs are considered as vulnerable marine ecosystems (Auster et al., 2011) that potentially provide very important ecosystem services. Consequently, around many CWC sites marine protected areas (MPA) have been established (e.g., off Norway and Ireland, around the Azores) to ban extraction of living and non-living resources invoking activities that are potentially harmful to the CWCs (e.g., Armstrong & van den Hove, 2008; Huvenne et al., 2016). However, MPA provide no protection against threats induced by ongoing global change (Jackson et al., 2014) such as ocean warming, acidification, deoxygenation and decreasing particulate organic matter fluxes to the seabed as these cannot be controlled locally (e.g., Sweetman et al., 2017). In addition, this range of environmental parameters might be even more critical for the proliferation or survival of CWCs considering a combined effect of multiple stressors (e.g., Büscher et al., 2017). Thus, to assess the vulnerability of CWCs to future global change, there is an indispensable need to comprehensively understand their sensitivity to changing environmental conditions.

The ecological requirements and tolerances of the most common framework-forming CWC species have been determined by field observations in the direct vicinity of CWC reefs (Dullo et al., 2008; Freiwald, et al., 2009; Brooke et al., 2013; Flögel et al., 2014) or by correlating their spatial occurrence to gridded data bank information describing the ambient environmental setting focusing mainly on physico-chemical properties of the water masses bathing the CWC reefs (Freiwald, 2002; Davies et al., 2008; Davies and Guinotte, 2011). Subsequently, the empirically obtained ranges of individual environmental parameters were interpreted as generally valid thresholds controlling the occurrence of CWCs on a global scale (Davies and Guinotte, 2011). However, recent discoveries of hitherto unknown CWC reefs that exist today under rather "extreme" conditions (e.g., in terms of temperature (Mienis et al., 2014) or oxygen (Ramos et al., 2017)), force us to shift the upper and lower thresholds of environmental parameters beyond formerly described values. In addition, laboratory experiments conducted on several common CWC species (e.g., *Lophelia pertusa*, *Madrepora oculata*, and *Dendrophyllia*) provided additional information on their ecological requirements (e.g., in terms of temperature, carbonate system, food supply, oxygen) (e.g., Tsounis et al., 2010; Gori et al., 2014; Movilla et al., 2014; Naumann et al., 2014; Maier et al., 2016; Büscher et al., 2017) and also indicate region-specific adaptations of CWCs to particular environmental parameters (Dodds et al., 2007; Lunden et al., 2014). Furthermore, exceeding/undercutting such environmental thresholds ("tipping point") causing a local extinction of CWCs has not been documented by field observations so far.

To overcome such lacking observations in order to further delineate the ecological tolerances of CWCs, here, a geological approach is followed. It enables the identification of CWC tipping points by taking advantage of the long-term development of CWC reefs. In the geological past, this often is marked by regional extinctions and re-occurrences of CWCs concomitant with changes in climate (e.g., Kano et al. 2007; Frank et al., 2011). Correlating such events, i.e. the crossing of tipping points, to the variability of paleoenvironmental parameters allows us to identify key parameters that potentially control the (regional) vitality of CWCs (e.g., Dorschel et al., 2005; Wienberg et al., 2010; Raddatz et al., 2014; Van der Land et al., 2014; Victorero et al., 2016).

Here, we outline this geological approach and provide the first comprehensive database of past environmental conditions (except ocean acidification) expected to have a potential impact on the spatial-temporal development of CWCs. The temporal focus is on the past ~20,000 years comprising the last major global warming event associated with the transition from the last glacial period to the present interglacial. To assess the sensitivity of CWCs to changing environmental conditions, we correlated selected paleoenvironmental parameters with on- and offsets of CWC reef growth in eight case studies from the North Atlantic Ocean and the Mediterranean Sea resulting in a comprehensive assessment of the sensitivity of CWCs to various environmental parameters. This provides pivotal information about the likely response of CWCs to those changes expected for the future. In the end, this information will allow the development and optimisation of management strategies for the sustainable protection of these important deep-sea ecosystems.

2. The concept

2.1 Tipping points crossed in the past

Over geological timescales of thousands to millions of years, CWCs can form coral mounds (composed of CWC fragments, shells of associated fauna, and hemipelagic sediments), which are widespread along the continental margins of the Atlantic Ocean (Wienberg and Titschack, 2017) reaching heights of up to >300 m (Mienis et al., 2006). The framework-forming CWC species mostly contributing to the formation of coral mounds are *L. pertusa*, *M. oculata*, *Solenosmilia variabilis*, *Bathelia candida*, and *Enallopsammia profunda* (e.g., Frank et al., 2011; Mangini et al., 2010; Munoz et al., 2012; Hebbeln et al., 2014). Coral mounds are distinct from the surrounding seafloor as they constitute elevated seabed structures causing enhanced hydrodynamics that support the supply of sediment and food particles. Therefore, coral mounds induce re-settlement of CWCs (that may develop into reefs) whenever the overall environmental settings turn favourable (Wienberg and Titschack, 2017).

Sediment cores obtained from coral mounds provide geological records allowing CWC vitality to be traced through time (e.g., Dorschel et al., 2005, Kano et al., 2007). For most coral mound sites investigated so far, it has been found that CWC records show alternating phases of coral vitality and absence (e.g., Eisele et al., 2008; Mienis et al., 2009; Matos et al., 2017). Precise dating by radiometric methods (e.g., uranium-series dating, radiocarbon dating) allows us to define the timing of (regional) extinction or re-occurrence of CWC and to relate these "tipping point crossings" with changes in environmental conditions (e.g., Frank et al., 2011) (Fig. 1).

Interestingly, the timing of crossing CWC tipping points, resulting in either their demise or their re-settlement in a given area, often coincides with major climatic changes. For many sites in the North Atlantic (e.g., off Norway, Ireland, and the US east coast, in the Mediterranean Sea and Gulf of Mexico), it has been found that after a long-lasting period (tens of thousands of years) of coral absence a re-settlement of CWCs occurred during the transition from the last glacial period to the present interglacial along with significant global warming (e.g., Frank et al., 2009; McCulloch et al., 2010; Taviani et al., 2011; López-Correa et al., 2012; Fink et al. 2015; Matos et al., 2015; 2017). However, the exact timing has been quite variable, for instance, starting relatively early at 14,000 years before present (BP) in the Mediterranean Sea (Fink et al., 2015; Stalder et al., 2015) and relatively late at 7,000 years BP off the US east coast (Matos et al., 2015). In contrast, off NW Morocco and Mauritania, CWCs flourished during glacial conditions and went regionally extinct concurrent with the global warming of the recent interglacial (Wienberg et al., 2010; 2018; Frank et al., 2011). This pattern of climate change-driven regional variations in coral proliferation is not just valid for the recent interglacial and last glacial (i.e. the last ~70,000 years), but can also be traced further back in time comprising previous glacial and interglacial stages (Frank et al., 2011; Raddatz et al., 2014; Van der Land et al., 2014; Matos et al., 2017; Wienberg et al., 2018). Beside major changes in CWC proliferation linked to glacial/interglacial climate variability, CWC development has regionally also been interrupted on shorter time scales, lasting for a few hundreds to thousands of years during interglacial or glacial periods (e.g., Fink et al., 2015, Raddatz et al., 2016; Wienberg et al., 2018).

2.2 Identifying key environmental drivers

To identify those environmental changes that are most likely the cause for the demise or re-settlement of CWCs, conventional paleoceanographic approaches can be used. At first glance, the aragonitic skeletons of the CWCs appear as the prime signal carrier for paleoceanographic changes. They provide an excellent, precisely datable paleoarchive offering a range of innovative proxies to reconstruct the paleoenvironment in which they thrived (Robinson et al., 2014). However, coral-based proxy records provide no environmental information on those times the corals were absent, thus precluding any before-and-after comparisons.

Therefore, the reconstruction of the paleoenvironment controlling the vitality of CWCs has to rely on sediment-based approaches. These can be applied either to the hemipelagic sediments deposited among the coral fragments on the coral mounds - so-called on-mound records - or to coral-barren sediments collected nearby, ideally from the same water depth to represent the same environmental setting, so-called off-mound records (Fig. 1; Dorschel et al., 2005). As the deposition of sediments within the coral framework can be somewhat patchy and is limited to the periods of coral growth (Thierens et al., 2013), the off-mound sites usually provide more continuous paleoenvironmental records (Dorschel et al., 2005; Rüggeberg et al., 2007; Wienberg et al., 2010; Fink et al., 2013).

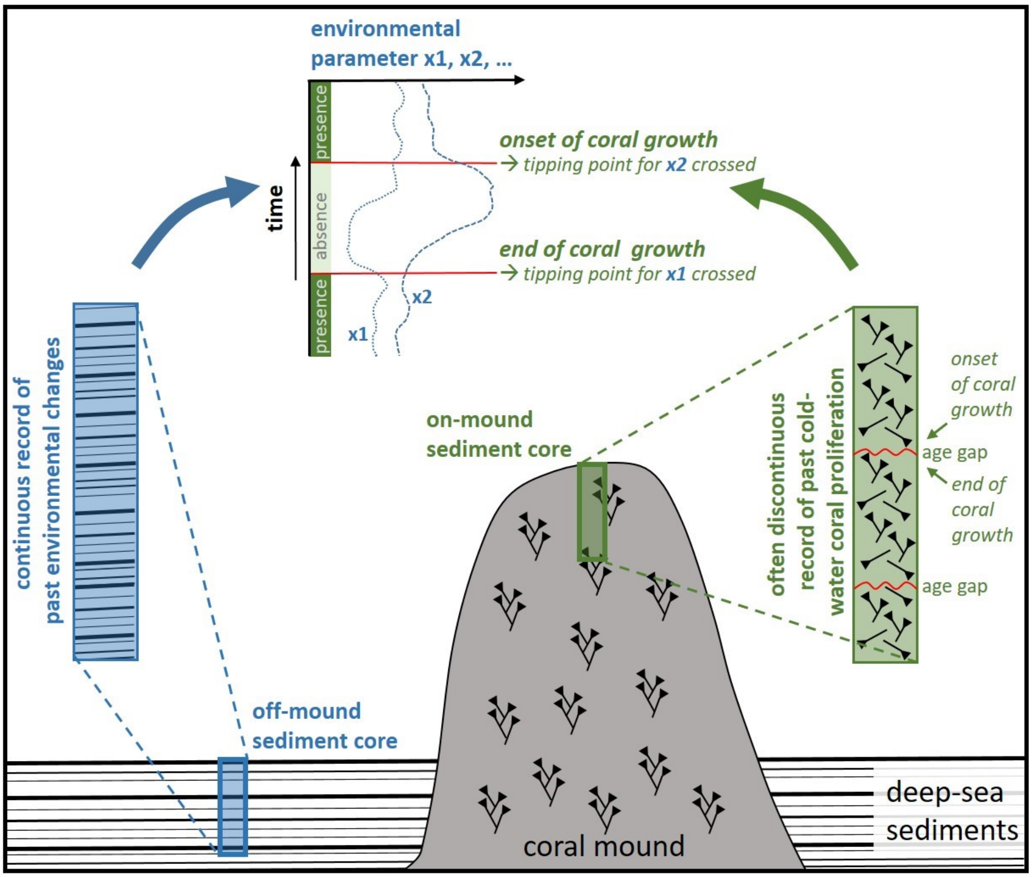

Fig. 1: Schematic presentation of the "geological approach" to assess the sensitivity of cold-water corals to environmental change and to identify the key ecological drivers being able to push cold-water corals across tipping points causing the demise/return of entire populations. By combining cold-water coral records retrieved from coral mounds with continuous paleoenvironmental records, such key drivers can be identified.

To assess the paleoenvironmental conditions controlling the proliferation of CWCs, various proxies can be applied to reconstruct past conditions at the seabed and within the bottom waters bathing CWC reefs. The most common paleoceanographic proxy carrier to describe past conditions at the seabed are benthic foraminifera. The chemical composition of their calcitic shells provides information, e.g., on bottom water temperatures (using Mg/Ca ratios, Lear et al., 2002) and salinities (by combining Mg/Ca-derived temperatures, Lear et al., 2002, with stable oxygen isotope data, Marchitto et al., 2014). To account for regional environmental differences and occurrences of benthic foraminifera species, the best fitting equations to estimate bottom water temperature and salinity have been selected from the literature (Tab. 1).

The surface productivity and organic matter export flux to the seafloor were inferred based on the benthic foraminifera accumulation rate (BFAR) expressed as the number of shells cm^{-2} ky^{-1} (Herguera and Berger, 1991). Increased abundance of benthic foraminifera has been positively correlated to regions and/or periods of enhanced chlorophyll and surface ocean biological production (Dias et al., 2018; Eberwein and Mackensen, 2006). The bottom water oxygenation was qualitatively estimated using elemental Mn/Ca ratios measured in benthic foraminifera shells (Groeneveld and Filipsson, 2013) and, in locations where benthic foraminifera assemblage data are available in the literature, we applied the Oxygen Index (OI) from Schmiedl et al. (2003). Besides the information gained from benthic foraminifera, the grain-size distribution of the terrigenous portion of the sediments (originating from river and wind input) allows reconstruction of the hydrodynamic conditions at the seabed (McCave et al. 2017). These were identified as being one critical parameter for the occurrence of CWCs beside productivity and the physical-chemical properties of the bottom waters (e.g., Davies et al., 2008), especially to further improve the (lateral) food delivery to the CWCs (Hebbeln et al., 2016).

Combining these proxies in a multi-proxy approach allows for a precise description of paleoenvironmental changes (Fischer and Wefer, 1999). However, although most of these proxies provide quantitative results describing former conditions, due to rather large error bars the results usually should be seen as semi-quantitative or sometimes only as qualitative estimates. Nevertheless, these records provide reliable archives of environmental change through time and linking these records with a pattern of coral presence and absence allows to pinpoint the most dramatic paleoenvironmental changes co-occurring with the on-set/off-set of CWC reefs. With such a multi-proxy approach, key environmental drivers pushing the corals across their tipping points can be identified as it is demonstrated in the case studies presented below.

Tab. 1: List of benthic foraminifera species-specific equations to estimate bottom water paleotemperature (BWT) and paleossalinity (BWS) as well as the $\delta^{18}O$ of seawater ($\delta^{18}O_{SW}$) ($\delta^{18}O_C$ refers to $\delta^{18}O$ measured on the foraminifera carbonate shells). The number in the left column refers to the regions presented in Fig. 2 to which the respective equations have been applied to. References: Shackleton, 1974 – (SK74), Lear et al., 2002 – (LE02), Cacho et al., 2006 – (CA06), Bryan & Marchitto, 2008 - (BM08), Huang et al., 2012 – (HU12), Marchitto et al., 2014 – (MA14) and Rüggeberg et al., 2016 – (RÜ16).

Region	Applied to species	Paleotemperature equation	Species calibration	Ref.	$\delta^{18}O_{SW}$ equation	Species calibration	Ref.	BWS-$\delta^{18}O_{SW}$ modern equation	Ref.
1	*Planulina ariminensis*	BWT=(LN(Mg/Ca/1))/0.08	*P. ariminensis*	BM08	$\delta^{18}O_{SW}=0.23*BWT-3.5+\delta^{18}O_C$	*Cibicidoides* spp	MA14	$BWS=(\delta^{18}O_{SW}+18.1)/0.5$	MA14
2	*Cibicides pachyderma*	BWT=(LN(Mg/Ca/0.87))/0.11	*Cibicidoides* spp	LE02	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)$	*Uvigerina* spp	SK74	$BWS=(\delta^{18}O_{SW}+18.1)/0.5$	MA14
3	*Cibicides* spp.	BWT=(LN(Mg/Ca/0.2))/0.184	*P. ariminensis*	HU12	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)+0.22$	*Cibicides* spp	HU12	$BWS=(\delta^{18}O_{SW}+15.4)/0.5$	RÜ16
4	*Uvigerina* spp	BWT= (Mg/Ca+0.7)/0.084	*Uvigerina* spp	BM08	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)$	*Uvigerina* spp	SK74	$BWS=(\delta^{18}O_{SW}+15.9)/0.5$	HU12
5	*P. ariminensis*	BWT=(LN(Mg/Ca/0.2))/0.184	*P. ariminensis*	HU12	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)+0.22$	*Cibicides* spp	HU12	$BWS=(\delta^{18}O_{SW}+15.9)/0.5$	HU12
6	*Cibicides mundulus*	BWT=(LN(Mg/Ca/0.61))/0.11	*Cibicidoides* spp	Ca06	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)$	*Uvigerina* spp	SK74	$BWS=(\delta^{18}O_{SW}+17.4)/0.5$	CA06
7	*C. mundulus*	BWT=(LN(Mg/Ca/0.61))/0.11	*Cibicidoides* spp	CA06	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)$	*Uvigerina* spp	SK74	$BWS=(\delta^{18}O_{SW}+17.4)/0.5$	CA06
8	*Uvigerina* spp	BWT=(LN(Mg/Ca/0.61))/0.11	*Cibicidoides* spp	CA06	$\delta^{18}O_{SW}=\delta^{18}O_C+(BWT-16.9/4)$	*Uvigerina* spp	SK74	$BWS=(\delta^{18}O_{SW}+17.4)/0.5$	CA06

3. The case studies – an overview

Such a geological approach has been followed in a number of studies, however, with varying sets of environmental parameters that have been reconstructed. Here we compile the available information from eight different regions that are distributed around the North Atlantic and the Mediterranean Sea (Fig. 2; Tab. 2). All these reconstructions already give some clear indications about key environmental drivers, which, however, can be regionally very different. However, a comprehensive approach with a similar set of proxies addressing the most likely critical environmental parameters for various CWC settings was so far missing. Thus, here we compiled existing data and generated new ones to generate such a comprehensive set of paleoenvironmental parameters that are expected to potentially play a key role in the development of CWC ecosystems: bottom water temperature, bottom water salinity, bottom water oxygenation, surface ocean productivity (organic material export to the sea floor) and the bottom water hydrodynamic regime (current speed controlling the lateral food supply to the CWCs). This dataset for the first time allows a comparison on the response of CWCs to environmental change in the past, considering in each region the same set of parameters. Difficult to cover by this geological approach are the effects of ocean acidification, as the younger geological history provides no equivalent to the acidic conditions expected until the end of this century.

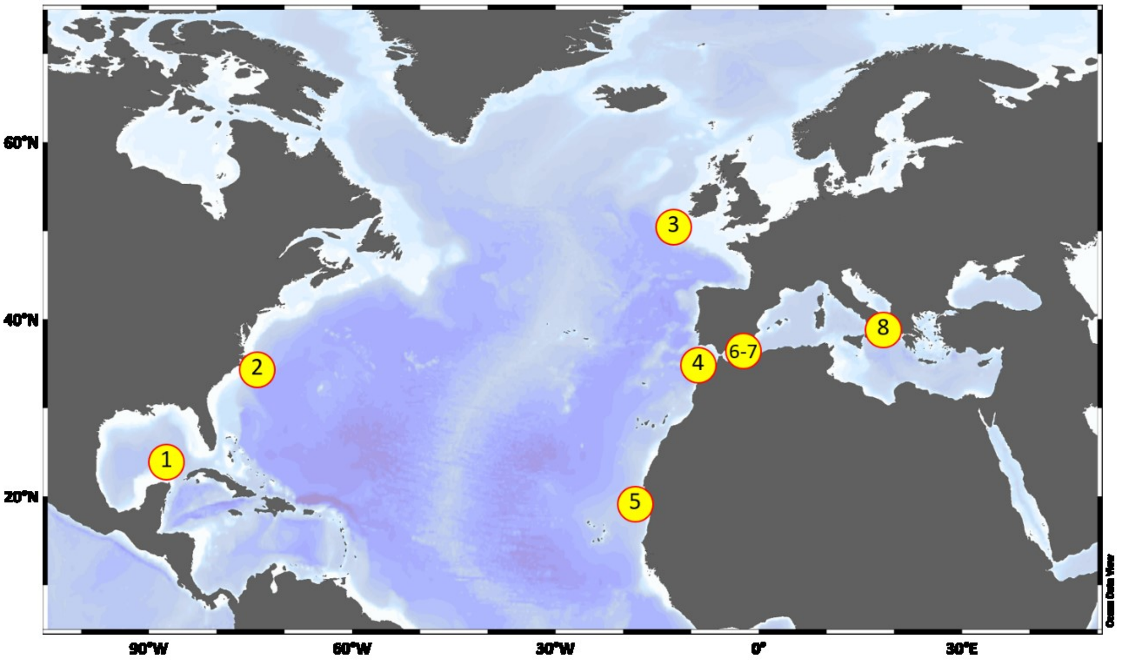

Fig. 2: Distribution of case study sites in the North Atlantic Ocean and in the Mediterranean Sea: (**1**) Campeche Province in Gulf of Mexico (Matos et al., 2017), (**2**) Cape Lookout (Matos et al., 2015), (**3**) Porcupine Seabight off Ireland (Dorschel et al., 2005, Frank et al., 2011), (**4**) Gulf of Cadiz (Wienberg et al., 2010), (**5**) Mauritanian margin (Eisele et al., 2011; Wienberg et al., 2018), (**6**) Western Melilla Mounds, Alboran Sea, (Wang et al., 2019) (**7**) Eastern Melilla Mounds, Alboran Sea (Fink et al., 2013), and (**8**) Santa Maria di Leuca Province, Ionian Sea - Eastern Mediterranean Sea (Fink et al., 2012). Figure created using Ocean Data View software (ODV - version, 4.7.9., http://odv.awi.de, 2018).

Tab. 2: Overview of the eight case study regions representing cold-water coral provinces in the North Atlantic Ocean and the Mediterranean Sea (the numbers in the leftmost column represent the regions in Fig. 2). Further information also about regional coral growth phases are provided in the references listed to the right.

	CWC site	Region	Latitude	Longitude	Water depth (m)	References
1	Campeche Province	Gulf of Mexico	23°83'N	87°15'W	626	Hebbeln et al. (2014), Matos et al. (2017).
2	Cape Lookout	NW Atlantic, US east coast	34°12'N	75°52'W	450	Mienis et al., 2014; Matos et al. (2015).
3	Porcupine Seabight	NE Atlantic, Irish margin	52°09'N	12°45'W	900	Dorschel et al. (2005), Rüggeberg et al. (2007)
4	Gulf of Cadiz	NE Atlantic	35°24'N	06°50'W	702	Wienberg et al. (2010)
5	Mauritanian margin	NE Atlantic	18°57'N	16°52'W	611	Wienberg et al. (2018), Titschack et al. (unpubl. data)
6	West. Melilla Mounds	Alboran Sea, Mediterranean	35°28'N	03°09'W	457	Wang et al. (2019)
7	East. Melilla Mounds	Alboran Sea, Mediterranean	35°19'N	02°34'W	251	Stalder et al. (2015), Fink et al. (2013)
8	Santa Maria di Leuca	Ionian Sea, Mediterranean	39°33'N	18°27'E	612	Fink et al. (2012)

In each of the individual case studies, which are detailed in the appendix, the paleoceanographic records have been linked to the occurrence of CWCs in order to pinpoint those environmental changes that co-occur with the crossing of major tipping points in the regional CWC development marked by their demise or their re-establishment (Fig. 1). In addition to the paleoceanographic proxies introduced above, these CWC records also have been compared to the global sea level curve (Grant et al., 2012; Waelbroeck et al., 2002).

4. Key environmental driver for CWC development

The major outcome of this approach is a multiple stressor matrix (Tab. 3), which combines all information from the eight case studies, for which the detailed regional response of the CWCs to environmental change is described in the appendix. In the multiple stressor matrix the roles of the selected environmental parameters as key drivers for the development of CWCs are differentiated into four categories: dominant role, strong role, some role, and no role (Tab. 3). A main finding is that temperature and salinity hardly played any role in controlling CWC proliferation through the last 20,000 years. Only in case study #4 (Gulf of Cadiz, Fig. A.4), a sudden short-term warming associated with an increase in salinity might have contributed to the demise of the CWCs approximately 9,000 years ago. In addition, in the Western Mediterranean Sea (case studies #6 and #7, Figs. A.6 and A.7), a strong decline in salinity during/slightly after the Younger Dryas cold event might have been unfavourable for the CWCs. However, it was rather the rapidly changing environment and, thus, the rather unstable conditions then the absolute salinity values that impacted on the CWCs.

Tab. 3: Multiple stressor matrix of environmental parameters controlling the occurrence of the cold-water corals in the North Atlantic and Mediterranean Sea over the last 20,000 years. Categories refer to dominant (+++, orange), strong (++, yellow), some (+, green) and no (-, blue) role of the individual parameters in controlling cold-water coral development,

Area	Bottom water temperature	Bottom water salinity	Bottom water hydro-dynamics	Surface ocean productivity	Bottom water oxy-genation	Sea level
Campeche Gulf of Mexico	-	-	+++	-	-	+
Cape Lookout off US east coast	-	-	+++	-	-	+
Porcupine Seabight Irish magin	-	-	+++	++	-	+
Gulf of Cadiz	+	+	++	++	-	+
Mauritanian margin	-	-	++	+++	-	+
Western Melilla, West. Mediterr. Sea	-	+	++	++	-	+
Eastern Melilla, West. Mediterr. Sea	-	+	++-	+++	+	+
Santa Maria di Leuca East. Mediterr. Sea	-	-	+	+	+++	-

no role	**some role**	**strong role**	**dominant role**

The limited role of temperature is in particular contrast to expectations regarding the possible impact of current and future ocean warming on CWCs (e.g., Lunden et al., 2014; Sweetman et al., 2017). This might be related to the fact that global change-induced temperature changes in those intermediate depths inhabited by CWCs are comparably small. Nevertheless, in regions where CWCs live close to their estimated upper temperature limit, as e.g., in the Mediterranean Sea, any future warming might prove fatal for them. Some case studies reveal changes in salinity in relation to the demise or re-establishment of CWCs, however, the absolute changes and levels appear not to be critical to the corals. More likely, the observed changes in salinity point to changes in water mass distribution, which might affect the hydrodynamic setting (e.g. internal waves along water mass boundaries; e.g., Matos et al., 2017) or the oxygen concentration (e.g., through water mass replacement; e.g., Wienberg et al., 2018).

Under specific conditions, bottom water oxygenation can be the main controlling driver for the CWCs. This becomes obvious from the Eastern Mediterranean Sea (case study #8, Fig. A.8), when a significant drop in oxygen associated with the Sapropel 1 event (de Lange et al., 2008) initiated a 4,000 year lasting interruption in CWC growth (Fink et al., 2012).

However, by far the most dominant environmental driver controlling CWC presence and absence in the investigated case study areas is food supply. For CWCs this depends mainly on two factors: the vertical supply of food particles resulting from primary production in the surface waters and the lateral supply governed by the strength of the bottom water hydrodynamic regime. Both factors are considered here independently and both jointly take strong and/or dominant roles in five of our eight case studies (#3 to #7; Figs. A.3 to A.7). Interestingly, in the two case studies #1 and #2 from the NW Atlantic changing hydrodynamic conditions appear to be the sole key environmental driver for CWCs (Figs. A.1 and A.2) (Matos et al., 2015; 2017).

Furthermore, the demise or re-establishment of CWCs appears in almost all case studies (except #8) to be linked to sea level as well, as most such changes occurred during major sea level changes. Yet, so far no process directly linking sea level with CWC proliferation has been identified. Thus, this link appears to be more an indirect one (e.g., vertical displacements of water masses boundary and associated nepheloid layers and internal waves) as major regional paleoenvironmental changes affecting the CWCs mostly occurred during reorganisations of the climate system (e.g., the last deglaciation), when sea level also underwent major changes.

5. Outlook

Combining observational data and multivariate statistical analyses has provided a wealth of information on ranges of individual environmental parameters tolerated by CWCs (e.g., Davies et al., 2008; Davies and Guinotte, 2011). In addition, laboratory experiments provided some insight into maximum and/or minimum tolerated levels of some environmental parameters (e.g., Tsounis et al., 2010; Gori et al., 2014; Movilla et al., 2014; Naumann et al., 2014; Maier et al., 2016; Büscher et al., 2017)), however, with partly contrasting results from different studies and areas (e.g., Dodds et al., 2007; Lunden et al., 2014) probably hinting at regional adaptations.

However, to what extent any reported environmental ranges define tipping points that upon crossing might cause the local/regional extinction of a population remains largely unanswered, in particular as during the observational/instrumental period no crossing of such an environmental tipping point for CWCs has been documented. By adding a geological perspective to this problem, the key environmental parameters that drove CWCs across such tipping points – either the demise or the re-establishment of CWC ecosystems – in the past can be identified. As mentioned above, the available data indicate food supply as the most prominent key driver. Thus, modeling projections on the ecological response of CWCs to future climatic changes should put a focus on the role of food supply depending on surface ocean productivity and the bottom water hydrodynamic regime. However, this observation also might point to a hidden impact of multiple stressors that often are energetically challenging for the metabolism of marine species, which potentially can be compensated by the availability of large quantities of high quality organic matter (Diaz and Rosenberg, 1995).

Consequently, in order to estimate the likely response of individual CWC species to those environmental changes expected up to the end of this century (and beyond), future geological as well as biological studies investigating their respective sensitivity need to consider the role of multiple stressors and possibly compensating factors. Of similar importance will be a better understanding of regionally varying tolerances of CWCs, a topic that just begins to emerge. In the future, a close cooperation of biologists, geologists and oceanographers to define the sensitivity of CWCs to environmental change, gives great potential to assess the fate of CWCs in the course of ongoing global change. Knowledge gained from such a cooperation will provide pivotal information to optimize strategies for the management of the unique deep-sea ecosystems formed by CWCs.

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7. Appendix

Detailed paleoceanographic records from the eight case studies investigated to assess the sensitivity of cold-water corals (CWC) to paleoenvironmental changes

A.1. The Campeche province in the southern Gulf of Mexico, Northwest Atlantic

The occurrence of CWCs in the Campeche Province (Fig. 2, Table 2) follows a glacial-interglacial pattern, with CWC growth observed during interglacials (i.e. the Holocene and the last interglacial) and their absence during glacial periods (Matos et al., 2017; Fig. A.1). Over the last 20,000 years the most prominent change for the CWCs is the re-establishment of the CWC reef at ~9 cal ka BP (see black dots on top of Fig. A.1).

The paleoceanographic data from off-mound core GeoB 16320-2 collected close to the observed living CWC reefs, reveal similar trends for bottom water temperature and salinity since 20 calendar kiloyears before present (cal ka BP), oscillating between ~7ºC and ~12ºC and between ~34 psu and ~36 psu, respectively (Fig. A.1A-B). Despite the relatively high amplitude of changes over this period (up to ~5ºC and 2 psu), both temperature and salinity did not show any significant changes and/or trends that align with the latest onset of CWC growth around ~9 cal ka BP indicating that these parameters had no controlling effect on the CWCs. The same applies for productivity with the benthic foraminifera accumulation rate (BFAR) showing almost no change around 9 cal ka BP, but a significant increase at 5 cal ka BP (Fig. A.1D). A more distinct signal is provided by the grain size data (here represented by the relative amount of the coarse silt fraction, 20-63 µm), which show a substantial coarsening of the sediments at the same time when CWC re-established in the region (Fig. A.1C). This strengthening of the local hydrographic regime reflected by the grain size data becomes even more evident when the record of the last 40 cal ka BP is considered (Matos et al., 2017). It probably triggered an enhanced lateral food supply allowing the suspension-filtering CWC to grow (Matos et al., 2017). Decreasing bottom water ventilation at 9 cal ka BP as indicated by the Mn/Ca ratios in the carbonate shells of benthic foraminifera (Fig. A.1E) most likely did not stimulate new coral growth. The Mn/Ca are rather low (<100µmol/mol), suggesting still well-ventilated bottom waters over the entire period, which is supported by an elevated abundance (>31%) of benthic foraminifera species adapted to high oxygen conditions (Matos et al., 2017). The re-establishment of CWCs in Campeche Province occurred during the last part of the deglacial sea level rise (Fig. A.1F).

Our results indicate that strengthened bottom water dynamics are the most crucial factor controlling the development of the CWCs in Campeche Province during the Early Holocene, most likely through increased lateral supply of food to the CWCs as suggested before (Matos et al., 2017). The strength of regional hydrodynamic regime at the seabed may be associated with the occurrence of interval waves linked to the deglacial return of the Antarctic Intermediate Water (AAIW) and the associated change in the vertical density gradient (Matos et al., 2017).

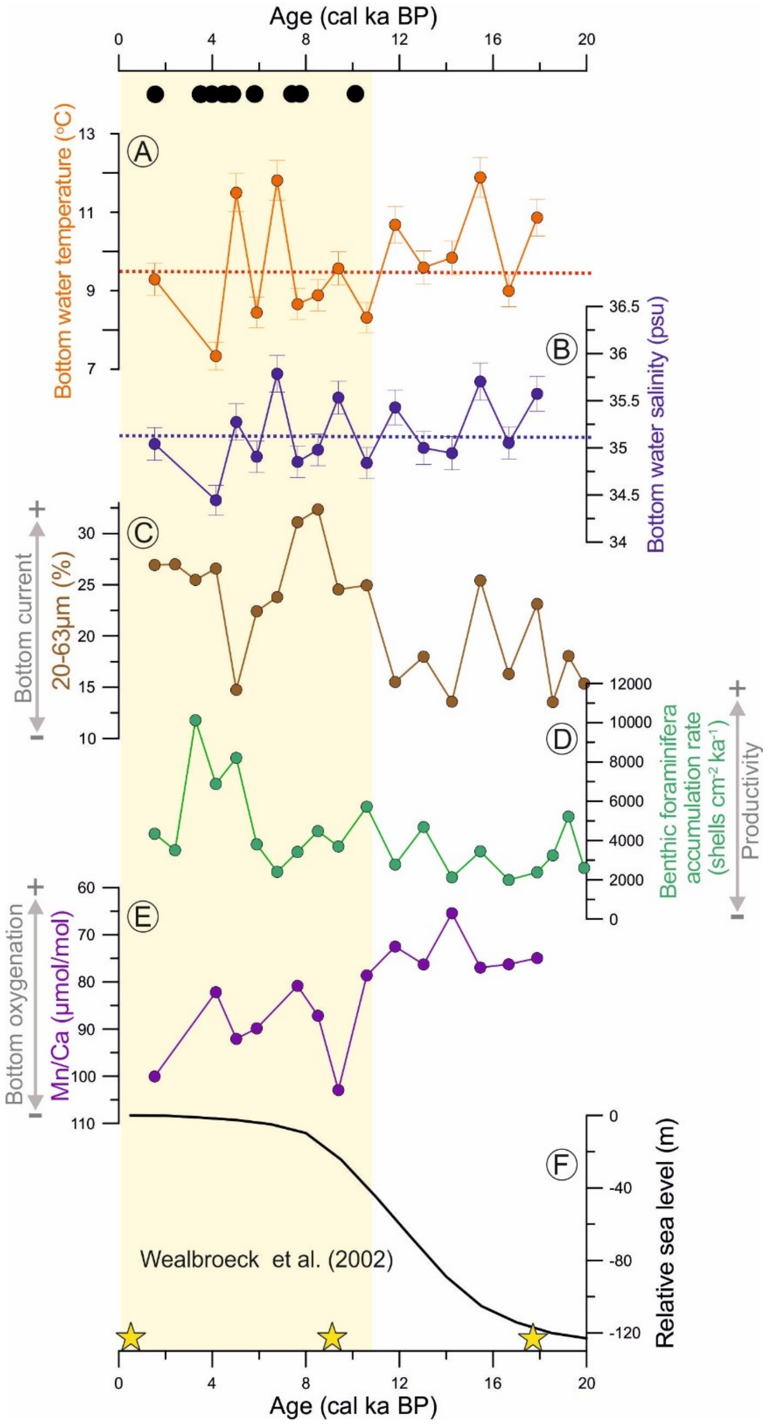

Fig. A.1: The paleoenvironmental history of the Campeche CWC Province in the southern Gulf of Mexico since 20 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Matos et al., 2017). The interval of CWC growth is marked by the yellow vertical bar. The paleoceanographic proxies have been obtained from the off-mound core GeoB 16320-2 (Matos et al., 2017). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the weight percentage of the coarse silt (20-63 µm) fraction (Matos et al., 2017). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Mn/Ca ratios measured on *P. ariminensis* are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Waelbroeck et al. (2002). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance with WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB 16320-2 are shown as yellow stars in the bottom (Matos et al., 2017).

A.2. The Cape Lookout site off the US east coast, Northwest Atlantic

Also in the Cape Lookout region (Fig. 2, Table 2) the occurrence of the CWCs follows a glacial-interglacial pattern, with CWC growth observed during interglacials (i.e. the Holocene and the last interglacial) and their absence during glacial periods (Matos et al., 2015; Fig. A.2). Over the last 20,000 years the most prominent change for the CWCs is the re-establishment of the CWC reef at ~7 cal ka BP (see black dots on top of Fig. A.2).

The paleoceanographic data from the off-mound core TRACOS2010-75 collected close to the observed living CWC reefs reveal relatively constant bottom water temperatures mainly oscillating between 6^{o}–8^{o}C (Fig. A.2A). The bottom water salinity showed a gradual increase from 34.8 psu to 36.1 psu between 20 and 8.3 cal ka BP (Fig. A.2B). While temperature shows no significant changes that align with the onset of CWC growth around ~7 cal ka BP, the increase in salinity already ended more than 1,000 years before the corals returned, thus, both parameters had seemingly no controlling effect on the CWCs. Furthermore, both, productivity reflected by the BFAR (Fig. A.2D) and bottom water oxygenation reflected by Mn/Ca (Fig. A.2E) provide rather low values after ~7 cal ka BP, which would point to a deterioration of the living conditions of the CWCs. Nevertheless, still low Mn/Ca values (<50 µmol/mol) indicate continuously well-ventilated bottom water over the entire period (Fig. A.2E). Thus, the onset of coral growth at this time probably is triggered by an intensification of the bottom water hydrodynamic regime as indicated by a drastic coarsening of the sediments ~7,000 years ago (Fig. A.2C) (Matos et al., 2015). The related positive effect on the lateral food supply to the CWC obviously outweighs the effect of decreasing productivity. The re-establishment of CWCs in Cape Lookout occurred when the deglacial sea level rise was almost complete (Fig. A.2F).

The results indicate that strengthened bottom water dynamics are the main factor controlling the re-establishment of CWCs in the Cape Lookout region during the Mid-Holocene, most likely through increased lateral food supply to the CWCs as suggested before (Matos et al., 2015). The strength of the regional hydrodynamic regime at the seabed may be linked to the strengthening of the Gulf Stream Current and its final on-shore displacement caused by the last bit of the deglacial sea level rise (Matos et al., 2015).

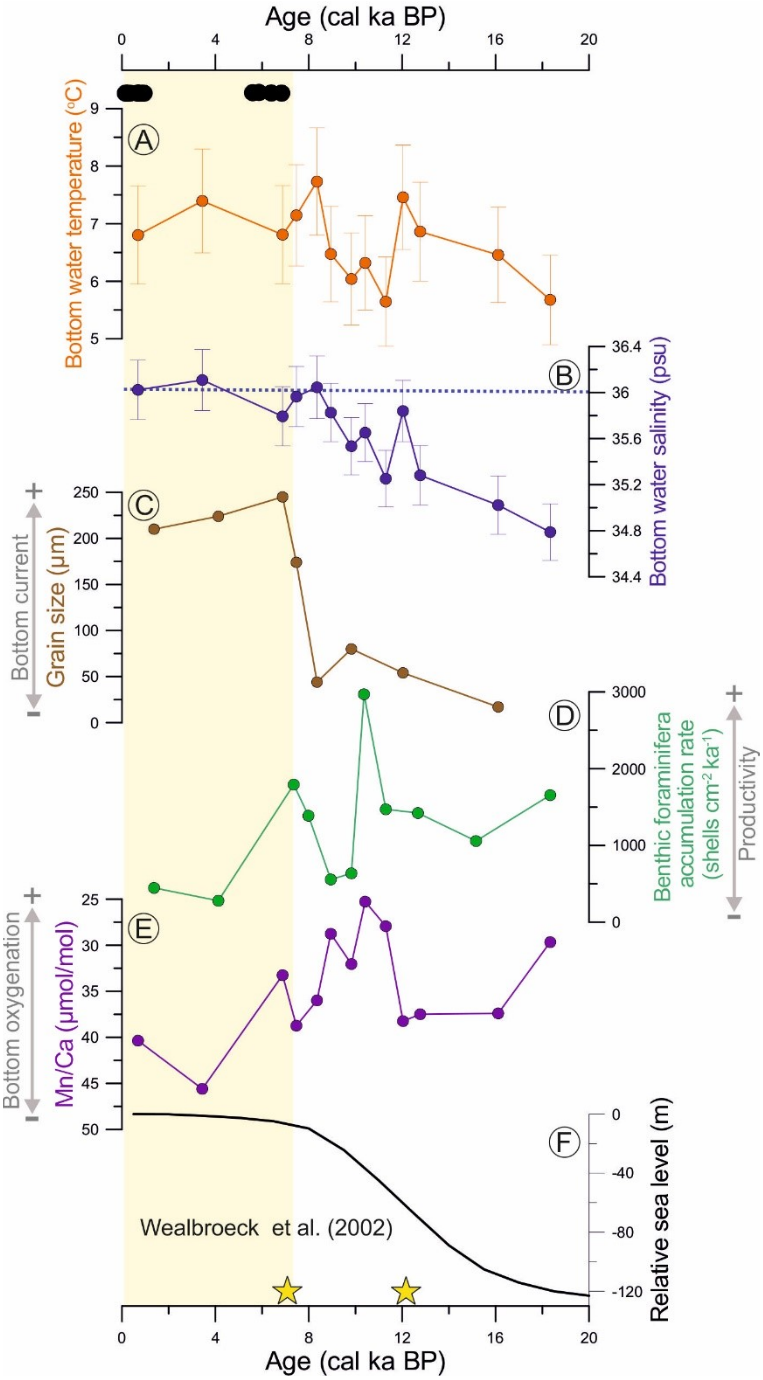

Fig. A.2: The paleoenvironmental history of the Cape Lookout CWC Province off the US east coast since 20 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Matos et al., 2015). The interval of CWC growth is marked by the yellow vertical bar. The paleoceanographic proxies have been obtained from the off-mound core TRACOS2010-75 (Matos et al., 2015). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired $\delta^{18}O$ and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size (Matos et al., 2015). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Mn/Ca ratios measured on *C. pachyderma* are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Waelbroeck et al. (2002). Horizontal dashed line in (**B**) indicates local modern annual salinity at the core site in accordance to WOA2013 (Zweng et al., 2013). Here it is noteworthy that the reconstructed bottom water temperatures are ca. 7–8°C lower than local modern annual values at this depth, therefore no dashed horizontal line was included in (**A**). Calibrated AMS ^{14}C ages for core TRACOS2010-75 are shown as yellow stars in the bottom (Matos et al., 2015).

A.3. The Propeller Mound in the Porcupine Seabight off Ireland, Northeast Atlantic

Propeller Mound in the Porcupine Seabight (Fig. 2, Table 2) is the third site marked by an glacial-interglacial occurrence pattern, with CWC growth observed during the present and former interglacials (Dorschel et al., 2005; Rüggeberg et al., 2007), a pattern typical for the entire Irish margin (Frank et al., 2011). Over the last 20,000 years the most prominent change for the CWCs is the re-establishment of CWC growth at ~11 cal ka BP (see black dots on top of Fig. A.3).

The paleoceanographic data from the off-mound core GeoB 6718-2 collected close to the observed living CWC reefs, reveal rather constant bottom water temperature, oscillating between 6°–8°C over the last 16 cal ka BP (Fig. A.3A). Bottom water salinity was >36 psu during the same period, except between 6 and 8 cal ka BP, when it dropped to values <35 psu (Fig. A.3B). However, around 11 cal ka BP, when CWCs returned, both parameters did not change significantly. Dissolved oxygen concentrations were relatively low over the last 16cal ka BP as indicated by benthic foraminifera Mn/Ca ratios >100 µmol/mol (Fig. A.3E). Even during a brief period between 6 and 8 cal ka BP, when Mn/Ca ratios increased to 500 µmol/mol pointing to a strong decline of oxygen levels in the bottom water, no impact on CWCs was found. Thus, also bottom water oxygenation most likely had no impact on the re-establishment of CWCs in Porcupine Seabight (Fig. A.3E). Major changes linked to the re-establishment of CWC at ~11 cal ka BP are the coarsening of the sediments indicating stronger bottom water dynamics (Fig. A.3C) and an increase of the BFAR (>2,000 shells cm^{-2} ka^{-1}) suggesting a higher surface productivity and an enhanced delivery of phytodetritus to the seabed (Fig. A.3D). Also the return of CWCs to the Irish margin took place during deglacial sea level rise (Fig. A.3F).

Thus, also for the Irish margin an enhanced delivery of food, driven by increasing bottom current velocities and by increasing surface water productivity and an associated vertical flux of organic matter to the seafloor, appears to be the crucial driver for the regional re-establishment of CWCs during the Holocene. This increased food supply probably is triggered by reduced sea ice coverage and the northward shift of oceanic fronts allowing northward incursions of the Mediterranean Outflow Water (Dorschel et al., 2005; Eisele et al., 2008; Frank et al., 2011; Rüggeberg et al., 2007).

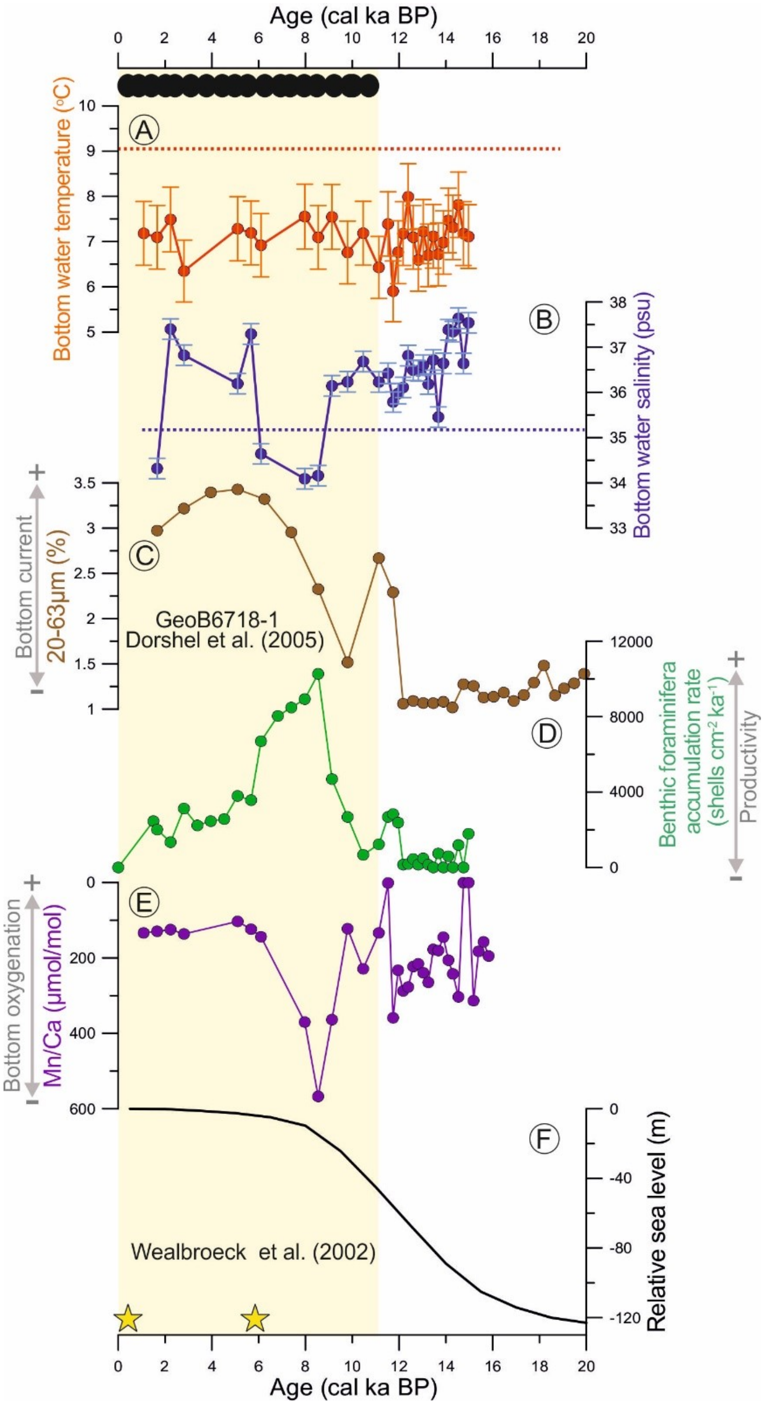

Fig. A.3: The paleoenvironmental history of the Porcupine Seabight CWC province at the Irish margin since 20 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Dorschel et al., 2005; Rüggeberg et al., 2007; Frank et al., 2011). The interval of CWC growth is marked by the yellow vertical bar. The paleoceanographic proxies have been obtained from the off-mound core GeoB 6718-2 (Dorschel et al., 2005; Rüggeberg et al., 2007). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the weight percentage of the coarse silt (20-63 µm) fraction (Dorschel et al., 2005). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Mn/Ca ratios measured on *Cibicides* spp. are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Waelbroeck et al. (2002). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB6718-2 are shown as yellow stars in the bottom (Dorschel et al., 2005).

A.4. The Gulf of Cadiz, Northeastern Atlantic Ocean

Like in other regions of the North Atlantic Ocean, the occurrence of CWCs in the Gulf of Cadiz (Fig. 2, Table 2) followed a glacial-interglacial pattern, however, marked by CWC growth during glacial periods and their absence during interglacial intervals (Wienberg et al., 2010; Frank et al., 2011). Over the last 20,000 years the most prominent change for CWCs is their regional demise at ~9 cal ka BP (see black dots on top of Fig. A.4).

The paleoceanographic data from the off-mound core GeoB 9064-1 located among numerous fossil CWC sites, show large fluctuations in bottom water temperature since 18 cal ka BP, ranging between 8°C and 14°C, with one anomalous peak of 17°C around 8 cal ka BP (Fig. A.4A). At this stage, this data point still needs to be confirmed by another measurement. Nevertheless, assuming it to be correct, it indicates temperatures higher than ~14°C corresponding to the reported upper limit of *Lophelia pertusa* (Roberts et al., 2009), which is one of the dominant CWC species in this region. This abrupt and extreme warming event almost concomitant with the end of CWC growth could have been the cause for the regional demise of CWCs. The bottom water salinity ranged between 34 psu and 37.5 psu, with a small decrease aligning with the demise of CWCs (Fig. A.4B), which, however, is well within the range of salinities tolerated by CWCs. As the temperature reconstruction goes into the calculation of the salinity, the peak in salinity coinciding with the peak in temperature at ~8 cal ka BP is no independent data point and, thus, has to be seen with caution. Low Mn/Ca values (<5µmol/mol) suggests very well-ventilated bottom waters over the entire period (Fig. A.4E). Decreasing mean grain sizes during the deglacial period indicate a weakening of the bottom currents and thus, decreasing lateral food supply to the CWCs (Wienberg et al., 2010) (Fig. A.4D). However, low values typical for the Holocene, when no CWCs lived in the area, were already reached by ~12 cal ka BP. Surface ocean productivity as reflected by the BFAR also decreased over the deglacial period, but reached lowest levels (BFAR <200 shells cm^2 ka^{-1}) only by ~4 cal ka BP (Fig. A.4D). In combination, both parameters point to decreasing food availability which might have crossed a certain threshold around ~11 cal ka BP. In contrast to the other regions of North Atlantic, in Gulf of Cadiz the CWC proliferation ended during the deglacial sea level rise (Fig. A.4F).

Summarising the results suggests that the continuously decreasing food availability at some point might have reached a critical level for CWCs. This can have caused their demise as proposed before (Wienberg et al., 2010) with the brief warming at ~8 cal ka BP possibly having set the final punch on the already weakened CWC community. Further paired Mg/Ca-δ^{18}O analyses in high-resolution are necessary to test the reliability of temperature and salinity peaks at 8 cal ka BP.

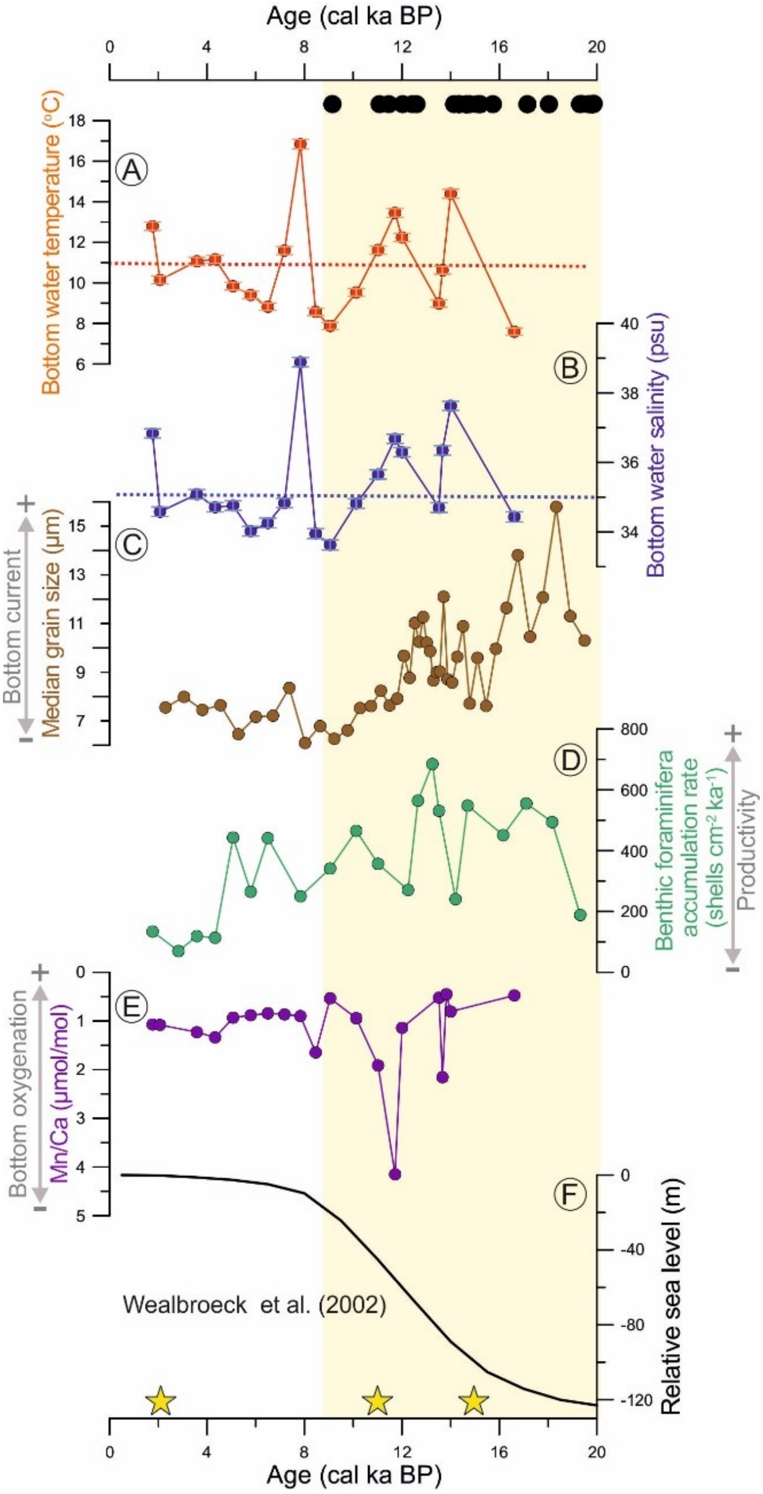

Fig. A.4: The paleoenvironmental history of the Gulf of Cadiz CWC province since 20 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Wienberg et al., 2009, 2010). The interval of CWC growth is marked by the yellow vertical bar. The paleoceanographic proxies have been obtained from the off-mound core GeoB 9064-1 (Wienberg et al., 2010). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size (Wienberg et al., 2010). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Mn/Ca ratios measured on *Uvigerina* spp. are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Waelbroeck et al. (2002). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB 9064-1 are shown as yellow stars in the bottom (Wienberg et al., 2009, 2010).

A.5. The Mauritanian Margin, Eastern Tropical Atlantic Ocean

The growth history of CWCs along the Mauritanian margin (Fig. 2, Table 2) followed the Gulf of Cadiz pattern, with CWC growth predominantly occurring during glacial intervals and their demise during the Holocene at ~9 cal ka BP (Eisele et al., 2011; Wienberg et al., 2018; Fig. A.5). In addition the CWC time series record from the Mauritanian margin reveals some millennial-scale response during the deglaciation phase as, e.g., their temporal demise coinciding with the Heinrich Stadial 1 (HS1; 14.7–18 cal ka BP) cold period (see black dots on top of Fig. A.5).

The paleoceanographic data from the off-mound core GeoB 14885-1 collected close the extended chains of cold-water coral mounds in this region, reveal rather constant bottom water temperatures oscillating between 8.5°–10.5°C over the last 20 cal ka BP (Fig. A.5A). Bottom water salinities show an increase of ~2 psu at the onset of HS1 and remain high (>36 psu) until mid-Holocene when it dropped to modern values after 3 cal ka BP (Fig. A.5B). Furthermore, fluctuating benthic foraminifera Mn/Ca ratios are not related to the absence/presence pattern of CWCs (Fig. A.5E). As temperature, salinity and oxygen conditions cover the full range of values during periods with and without coral growth, these parameters most likely had no controlling effect on CWC growth of Mauritania. The mean grain size data reveal a distinct trend of decreasing bottom water hydrodynamics from 20 cal ka BP until 3 cal ka BP (Fig. A.5C), which could explain the absence of CWCs after ~9 cal ka BP, however, without providing any clue for the gap in coral growth during HS1. The most distinct proxy signal with respect to the CWC occurrence pattern is provided by the BFAR and, thus, by the surface ocean productivity. The close link between high productivity (BFAR > 10,000 shells cm^{-2} ka^{-1}) and CWC presence and low productivity (BFAR < 9,000 shells cm^{-2} ka^{-1}) and CWC absence (Fig.A.5D) provides a clear hint that the temporal variability of the primary production played a crucial role in development of CWCs along the Mauritanian margin over the last 20,000 years. Similarly to the Gulf of Cadiz, the final coral demise during the Holocene coincided with the final sea level rise in the course of the last deglaciation (Fig. A.5F).

In general, the development of CWCs at the Mauritanian margin appears to be closely connected to the food supply associated with temporal and spatial variability of the upwelling system off NW-Africa (Eisele et al., 2011). The final demise of CWCs at ~9 cal ka BP might also be affected by the loss of hydrodynamic energy at this time further reducing the lateral food supply. In addition, there is evidence that occurrence of CWCs in the Mauritania margin is related to large-scale changes in geometry of the thermocline water masses (North Atlantic Central Waters versus South Atlantic Central Waters), which might have been an important factor for the demise of CWCs during HS1 (*cf.* Wienberg et al., 2018).

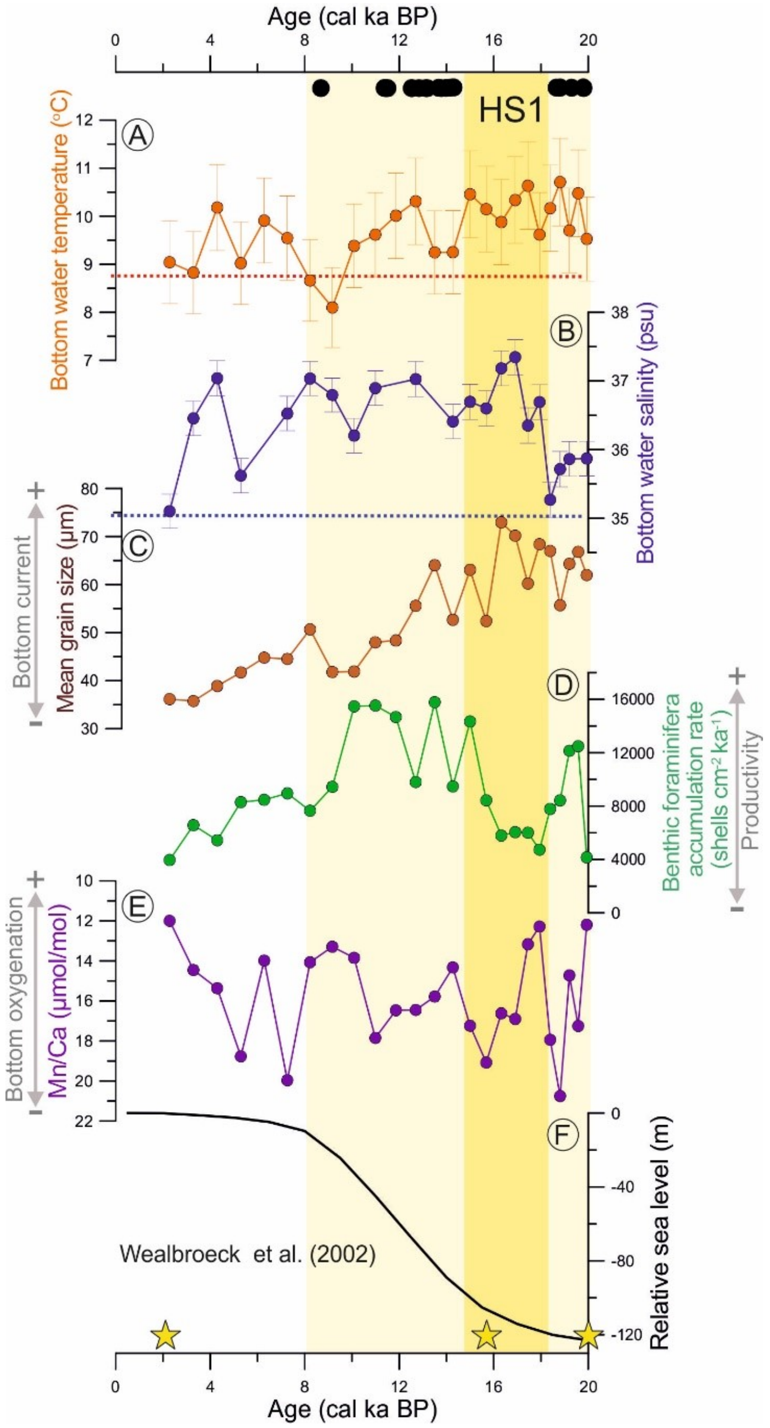

Fig. A.5: The paleoenvironmental history of the Mauritanian CWC province over the last 20cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Eisele et al., 2011; Wienberg et al., 2018). The interval of CWC growth, marked by the light yellow vertical bar, is interrupted during the Heinrich Stadial 1 (HS1), marked by the deep yellow bar. The paleoceanographic proxies have been obtained from the off-mound core GeoB 14885-1 (Wienberg et al., 2018). (**A**) Bottom water tempera-ture is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired $\delta^{18}O$ and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size. (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Mn/Ca ratios measured on *P. ariminensis* are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Waelbroeck et al. (2002). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB 14885-1 are shown as yellow stars in the bottom.

A.6. The Western Melilla Mound –in Alboran Sea, Western Mediterranean Sea

Following their absence during glacial times, the return of CWCs to the Mediterranean Sea occurred at ~14 cal ka BP (Fink et al., 2015; McCulloch et al., 2010). In the Western Melilla Mound (WMM) province, Alboran Sea (Western Mediterranean Sea) (Fig. 2, Table 2), CWCs developed predominantly between ~14 and 8 cal ka BP with a local demise event during the Younger Dryas cold period (YD; 11.7–12.8 cal ka BP; Wang et al., 2019) (see black dots on top of Fig. A.6).

The paleoceanographic data from the off-mound core GeoB 18131-1 obtained from close to the coral mounds, reveal relatively constant bottom water temperatures ranging between 9°C and 11°C between 20 cal ka BP and 6 cal ka BP (Fig. A.6A) with no significant changes and/or trends that align with the establishment of CWC growth around ~14 cal ka BP and/or CWC demise during the YD and after 8 cal ka BP. The bottom water salinity displayed a sharp decrease of 5 psu after 13 cal ka BP (Fig. A.6B). Although this coincides with the short-term demise of CWCs during the YD, CWCs were thriving under the highest (~41 psu at ~14 cal ka BP) as well as under the lowest salinities (~36 psu at ~9 cal ka BP) of the record, disproving a major impact of this parameter. At ~14 cal ka BP the benthic foraminifera Mn/Ca values indicate a decrease in bottom water oxygenation (Fig. A.6E), which most likely was not the trigger for the onset of coral growth at this time. In contrast, again the food supply appears to be the main trigger for coral growth: an increased BFAR since ~14 cal ka BP suggests high surface productivity and enhanced amounts of phytodetritus reaching the seafloor (Fig. A.6D) while at the same time coarser mean grain sizes (Fig. A.6C) point to strong hydrodynamics supporting the lateral food supply. Both parameters show a slightly different pattern, indicating first the strengthening of the bottom current regime reaching a maximum at ~12 cal ka BP that is followed by a maximum surface productivity (up to 27,000 shells cm^{-2} ka^{-1}) lasting from 11 cal ka BP to 8 cal ka BP. But most importantly, low values of both parameters coincide with the periods of CWC absence. However, this does not apply to the brief YD period also marked by the absence of CWCs. The most prominent environmental change associated with the YD is the sudden drop in salinity, probably triggered by a reorganization of the water column structure induced by a fast rising sea level at this time (Fig. A.6F). Although the absolute salinities seemingly cause no problem to CWCs, the fast change taking place during this period might have been unfavourable for their development.

These results show that an enhanced delivery of food caused by elevated surface productivity and increased lateral food supply were the key environmental drivers for the regional development of CWCs in the Western Melilla Mound province. The brief demise of CWCs during the YD might be related to rather unstable environmental conditions related to a major reorganization of the water mass structure in the Alboran Sea.

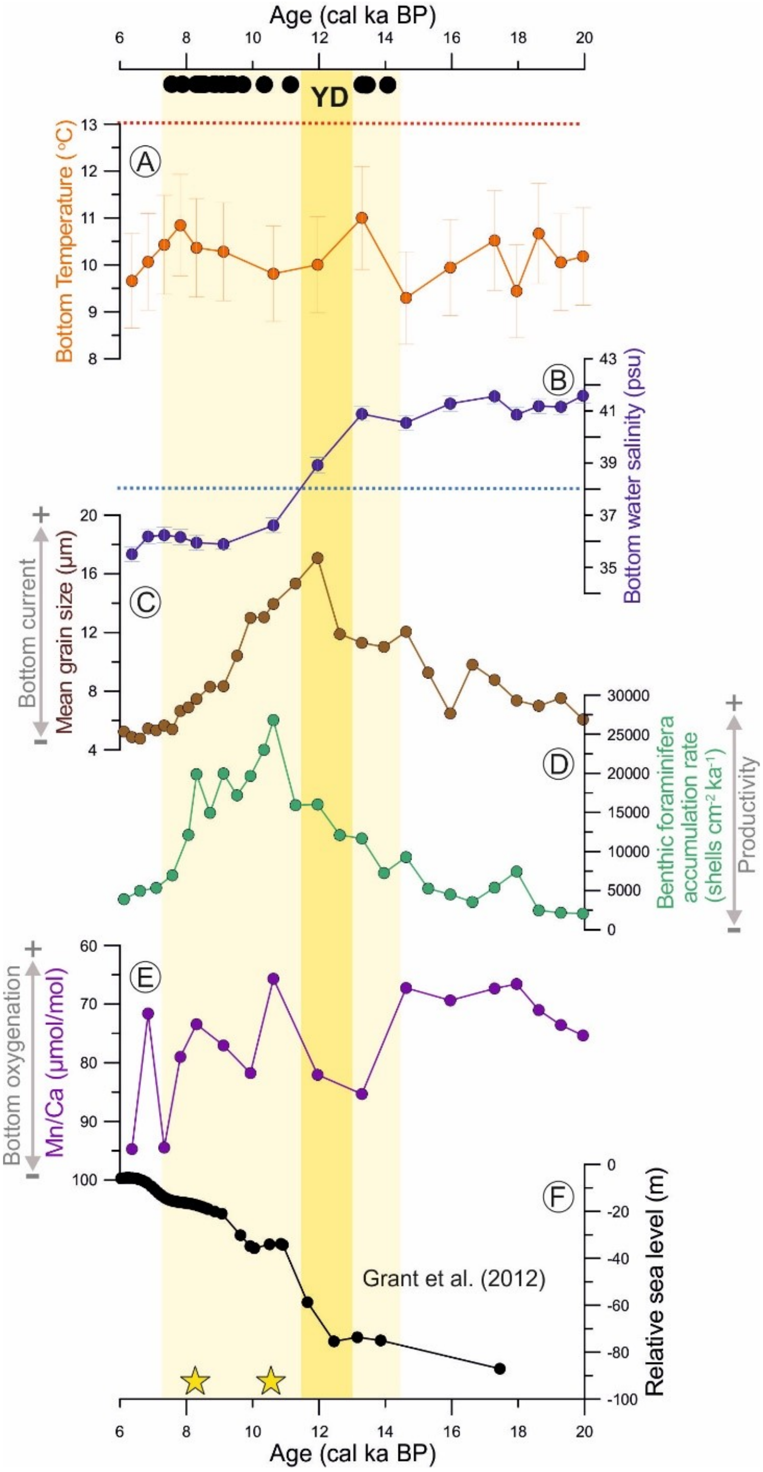

Fig. A.6: The paleoenvironmental history of the West Melilla Mound province in the Alboran Sea (Western Mediterranean) between 20 cal ka BP and 6 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Wang et al., 2019). The interval of CWC growth, marked by the light yellow vertical bar, is interrupted during the Younger Dryas cold event (YD), marked by the deep yellow bar. The paleoceanographic proxies have been obtained from the off-mound core GeoB 18131-1 (Wang et al., 2019). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for equations see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size (Wang et al., 2019). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting (Wang et al., 2019). (**E**) Mn/Ca ratios measured on *C. mundulus* are a proxy for bottom water oxygenation (note the inverse axis). (**F**) Relative sea level curve from Grant et al. (2012). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB 18131-1 are shown as yellow stars in the bottom (Wang et al., 2019).

A.7. The East Melilla Mound in Alboran Sea, Western Mediterranean Sea

CWC development in the in Eastern Melilla Mound province in the Alboran Sea (Western Mediterranean Sea) followed a similar pattern as found in its neighbouring western mound province (see A.6) with a distinct CWC growth period lasting from ~14 cal ka BP until ~9 cal ka BP with a brief interruption during the YD (Fink et al., 2013; see black dots on top of Fig. A.7).

The paleoceanographic data from off-mound core the GeoB 13731-1 collected close to the coral mounds, show also for this province relatively constant bottom water temperatures between 15 cal ka BP and 6 cal ka BP oscillating between 10°C and 14°C (Fig. A.7A). Despite the high amplitude of changes (up to ~4°C), the temperature did not show any significant changes and/or trends that align with the on- and offsets of CWC growth. The salinity record shows a decline of 4 psu between the YD (~40 psu) and the early Holocene (~36 psu) (Fig. A.7B). Compared to the Western Melilla Mound province this major shift in salinity appears slightly delayed here, which might be due to an offset of ~100 m between the water depth levels of the two off-mound cores. Nevertheless, also in the Eastern Melilla Mound province CWCs occur at times marked by highest as well as by lowest salinity levels, excluding any major impact of salinity on their proliferation. Again, also here the two parameters related to food supply agree best with the presence/absence pattern of CWCs: the bottom water hydrodynamic regime inferred by the mean grain size suggests strong bottom currents especially in the first part of the CWC growth period, i.e., between 14 cal ka BP and 10 cal ka BP (Fig. A.7 C), whereas surface ocean productivity indicated by the BFAR reveals highest values between 10 cal ka BP and 8.5 cal ka BP (>16,000 shells cm^{-2} ka^{-1})(Fig. A.7D). The demise of CWC during the YD might be related to a slightly reduced productivity (BFAR: ~8,000 shells cm^{-2} ka^{-1}) (Fig. A.7D) or, like in the Western Melilla Mound province, to changes in the water column structure induced by a fast rising sea level (Fig. A.7F). The most prominent signal in the record of dissolved oxygen concentrations at the seabed, here estimated using the oxygen index based on benthic foraminifera assemblages preserved in nearby core TTR17-401G (Stalder et al., 2015), is a strong decline in oxygenation between 11 cal ka BP and 9 cal ka BP(Fig. A.7E) partly matching the onset of the Sapropel (S1) layer formation in the Eastern Mediterranean Sea (de Lange et al., 2008).

These results confirm that enhanced delivery of food associated to vigorous bottom water current and elevated flux of organic matter to the seafloor were crucial to the development of CWCs in this region between 14 cal ka BP and 9 cal ka BP (Fink et al., 2013). However, at least for the demise of CWCs at ~9 cal ka BP a decrease in bottom waters oxygenation also might have played a role, although the minimum oxygen levels seemingly were reached before the final demise.

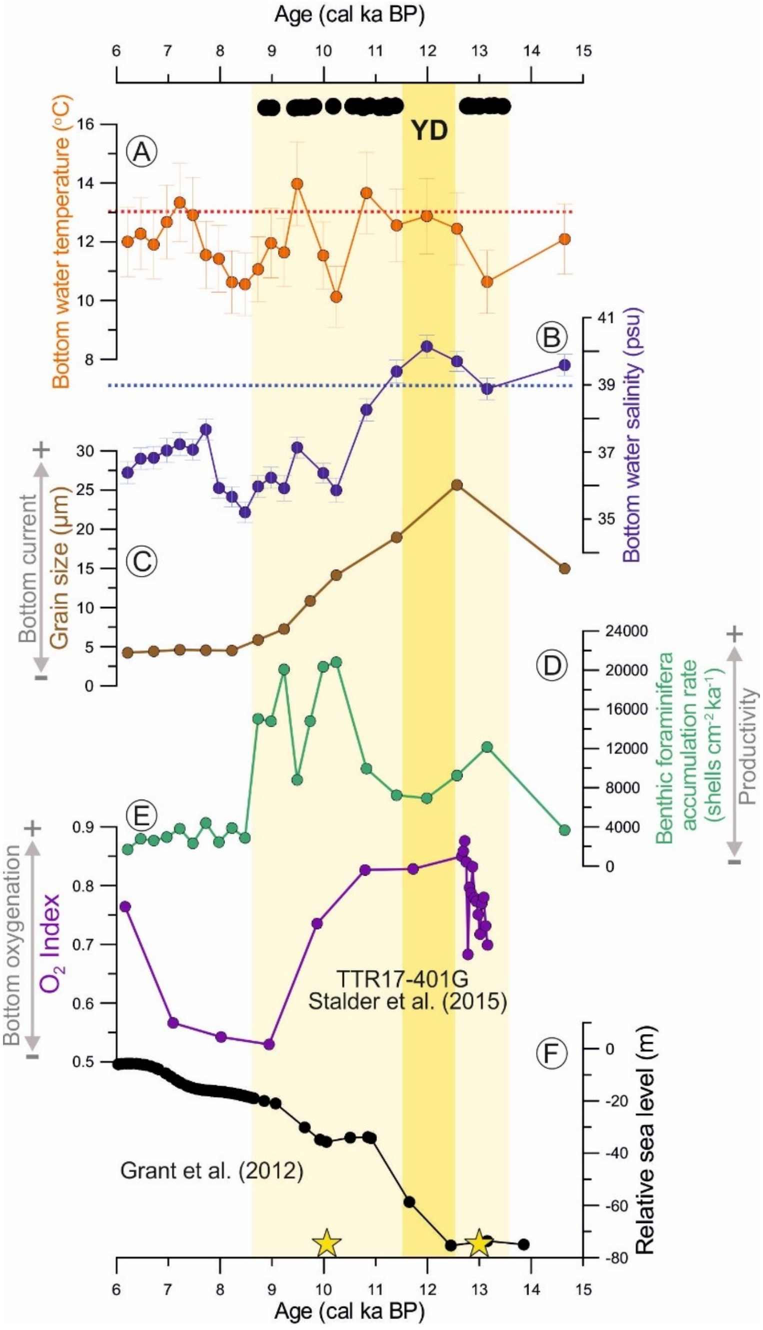

Fig. A.7: The paleoenvironmental history of the East Melilla Mound province in the Alboran Sea (Western Mediterranean) between 15 cal ka BP and 6 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the U/Th method (Fink et al., 2013, 2015). The interval of CWC growth, marked by the light yellow vertical bar, is interrupted during the Younger Dryas cold event (YD), marked by the deep yellow bar. Most paleoceanographic proxies have been obtained from off-mound core GeoB 13731-1 (Fink et al., 2013). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size (Fink et al., 2013). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Bottom water oxygenation is based on the Oxygen Index applied to benthic foraminifera assemblages from nearby core TTR17-401G (Stalder et al., 2015). (**F**) Relative sea level curve from Grant et al. (2012). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages for core GeoB 13731-1 are shown as yellow stars in the bottom (Fink et al., 2013).

A.8. The Santa Maria di Leuca Province (Ionian Sea), Eastern Mediterranean Sea

The occurrence of CWCs in the Santa Maria di Leuca Province in the Ionian Sea (Eastern Mediterranean Sea) (Fig. 2, Table 2) is limited to the last 12,000 years, however with a prominent gap between 10 cal ka BP and 6 cal ka BP (see black dots on top of Fig. A.8; Fink et al., 2012). This gap coincides with the formation of the Sapropel 1 (S1) event in the Eastern Mediterranean Sea marked by a strong reduction of bottom water oxygenation, especially in the deepest basins (de Lange et al., 2008).

The paleoceanographic data from on-mound core GeoB 11186-1 reveal a rapid warming of ~5°C of the bottom water after 12 cal ka BP, which remained high (11°C-16°C) until ~9.5 cal ka BP. Following a rather stable period of ~12°C, temperatures dropped to 10°C-11°C at 6 cal ka BP (Fig. A.8A). The bottom water salinity showed an overall decreasing trend from 43 psu to 37 psu during the Holocene (Fig. A.8B). CWCs co-occurred with the highest as well as with the lowest temperatures and salinities observed, indicating that these parameters had no controlling effect on local CWC development. A major decrease of the mean grain size at ~10 cal ka BP indicates a reduction in bottom water hydrodynamics and, thus in the lateral delivery of food, that actually coincides with the demise of CWCs (Fig. A.8B-C). However, continuously small mean grain sizes coincide with the presence of CWCs after 6 cal ka BP making a decisive impact of the hydrodynamics on CWC proliferation in this region unlikely. The BFAR shows an opposite pattern with low values (<1,000 shells cm^{-2} ka^{-1}) before 6 cal ka BP and high values (>1,000 shells cm^{-2} ka^{-1}) thereafter (Fig. A.8D). It cannot be excluded here that combined low mean grain size and BFAR values between 10 cal ka BP and 6 cal ka BP are linked to the absence of CWCs during this time and that before and after alternatively either the hydrodynamic regime or the surface ocean productivity triggered CWC growth. However, seeing the overall rather low values also compared to the other case studies, a controlling role of food supply on CWC development probably can be excluded. In contrast, in the Santa Maria di Leuca Province the decline of CWCs between 10 cal ka BP and 6 cal ka BP appears to be intimately linked to poorly-ventilated bottom waters as evidenced by the Oxygen Index (OI) derived from benthic foraminifera assemblage from nearby off-mound core SA03-1 (Fig. A.8E; Tesi et al., 2017). As mentioned before, this period coincides with the Sapropel 1 event, when the deep eastern Mediterranean Sea became even anoxic with similar, yet less extensive impacts on the intermediate waters (de Lange et al., 2008). Finally, the sea level record reveals no obvious link to CWC development in this region (Fig. A.8.F).

These records show that in the Santa Maria di Leuca Province oxygen concentration of the bottom waters is the most critical environmental parameter controlling the development of CWC during the Holocene.

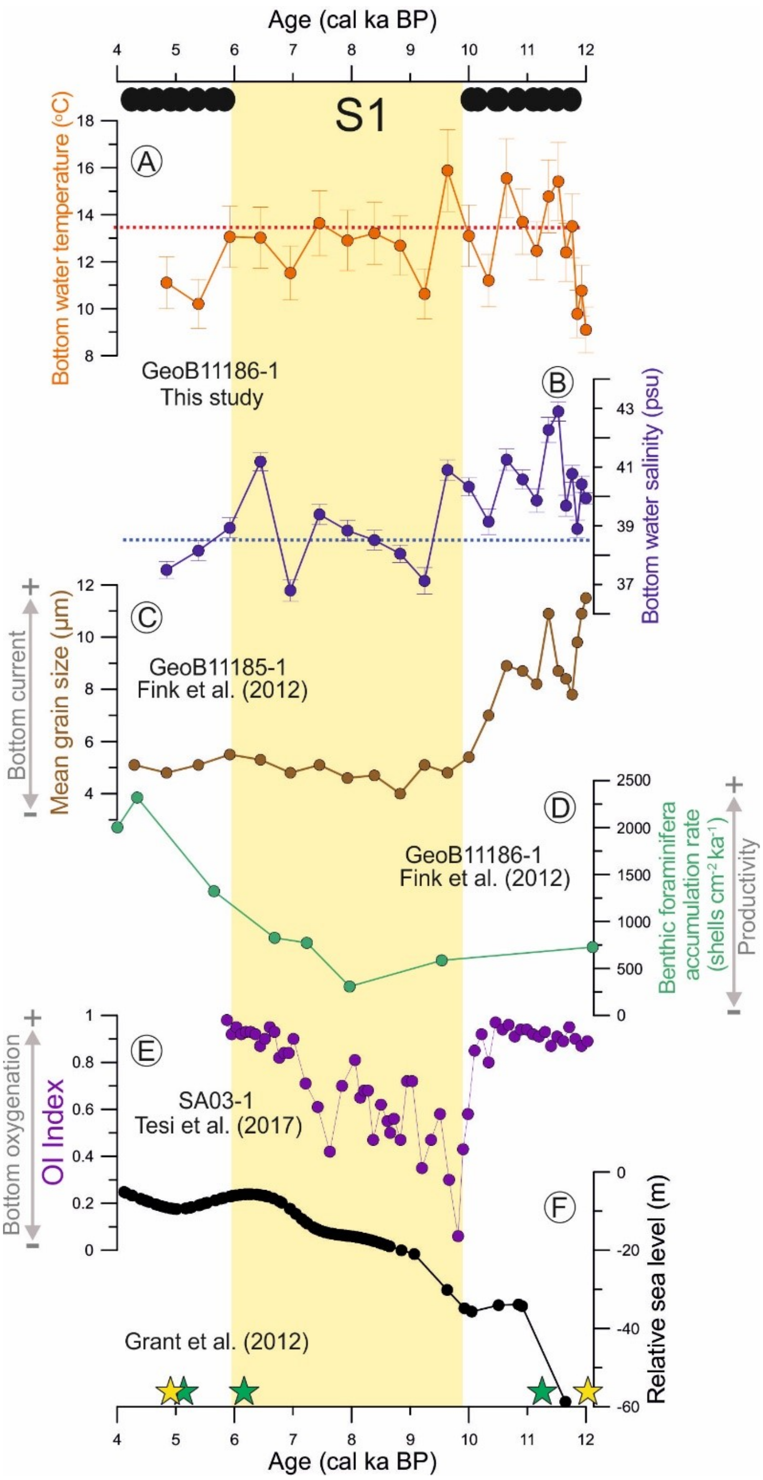

Fig. A.8: The paleoenvironmental history of the Santa Maria di Leuca Province in the Ionian Sea (Eastern Mediterranean) between 12 cal ka BP and 4 cal ka BP. The occurrence of CWCs in the region is indicated by black dots at the top reflecting coral fragments dated by the ^{14}C method (Fink et al., 2012). The interval of CWC absence is marked by the yellow vertical bar. Most paleoceanographic proxies have been obtained from the on-mound core GeoB 11186-1 (Fink et al., 2012). (**A**) Bottom water temperature is based on Mg/Ca ratios (for details see Table 1). (**B**) Bottom water salinity is based on paired δ^{18}O and Mg/Ca measurements (for details see Table 1). (**C**) The grain size record as a proxy for the bottom current strength represents the mean grain size (Fink et al., 2012). (**D**) The benthic foraminifera accumulation rate as a proxy for surface ocean productivity is based on foraminifera counting. (**E**) Bottom water oxygenation is based on the Oxygen Index from Schmiedl et al. (2003) applied to benthic foraminifera assemblages of nearby off-mound core SA03-01 (Tesi et al., 2017). (**F**) Relative sea level curve from Grant et al. (2012). Horizontal dashed lines in (**A**) and (**B**) indicate local modern annual values of temperature (red) and salinity (blue) at the core site in accordance to WOA2013 (Locarnini et al., 2013; Zweng et al., 2013). Calibrated AMS ^{14}C ages from cores GeoB 11185-1 (yellow stars) and GeoB 11186-1 (green stars) are shown in the bottom (Fink et al., 2012).

Appendix: Document Information

EU Project N°	678760	**Acronym**	ATLAS
Full Title	A trans-Atlantic assessment and deep-water ecosystem-based spatial management plan for Europe		
Project website	www.eu-atlas.org		

Deliverable	**N°**	D1.4	**Title**	Deep-sea ecosystem tipping points
Work Package	**N°**	1	**Title**	Ocean Dynamics Driving Ecosystem Response

Date of delivery	**Contractual**
Dissemination level	Confidential

Authors (Partner)	**UniHB**			
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Version log			
Issue Date	**Revision N°**	**Author**	**Change**