



Thousands of cold-water coral mounds along the Moroccan Atlantic continental margin: Distribution and morphometry

Dierk Hebbeln^{a,*}, Maren Bender^a, Stefanie Gaide^a, Jürgen Titschack^{a,b}, Thomas Vandorpe^c, David Van Rooij^d, Paul Wintersteller^a, Claudia Wienberg^a

^a MARUM – Center for Marine Environmental Sciences, University of Bremen, Leobener Straße 8, 28359 Bremen, Germany

^b Senckenberg am Meer, Marine Research Department, Wilhelmshaven 26382, Germany

^c VLIZ – Flanders Marine Institute, Wandelaarkaai 7, 8400 Oostende, Belgium

^d Ghent University, Department of Geology, Renard Centre of Marine Geology, Campus Sterre S8, Krijgslaan 281, 9000 Ghent, Belgium

ARTICLE INFO

Editor: G.J. de Lange

Keywords:

Cold-water corals
Coral mounds
NW African margin
Internal waves
Carbonate budget

ABSTRACT

Coral mounds formed by framework-forming cold-water corals pierce the seabed along most continental margins of the Atlantic Ocean and new sites are continuously being discovered. Here, we describe an extremely high accumulation of coral mounds at the NW Moroccan Atlantic margin between 35°N and 35.5°N. Within an area of only 1440 km², > 3400 mounds were found exposed at the seabed. The coral mounds are nowadays characterized by an almost complete lack of living cold-water corals. In addition, numerous buried mounds were identified in hydroacoustic sub-bottom profiles, and are estimated to be ~3.7 times more frequent than the exposed mounds. Consequently, a total of ~16,000 buried and exposed mounds is estimated for the entire study area. The exposed mounds are rather small with a mean height of 18 m and show a conspicuous arrangement in two slope-parallel belts that centre in water depths between 720 and 870 m and 890–980 m, respectively, putting them among the deepest mound occurrences discovered so far in the Atlantic. The mostly elongated mounds largely stretch downslope pointing to a significant influence of internal waves in the mound formation process. Moreover, based on their average dimensions, the entire coral mound volume can be estimated as 1.3 km³, which means the mounds store a considerable amount of coral carbonate highlighting their potentially important role as regional carbonate factories. In combination with further occurrences of coral mounds along the Moroccan margin, both in the Mediterranean and in the Atlantic Ocean, these new findings underline Morocco's role as a hotspot for the occurrence of cold-water coral mounds.

1. Introduction

Coral mounds, created by scleractinian framework-forming cold-water corals, are ubiquitous seabed features along the continental margins of the Atlantic Ocean and its adjacent marginal seas such as the Mediterranean Sea and the Gulf of Mexico (Hebbeln and Samankassou, 2015; Henriët et al., 2014; Wienberg and Titschack, 2017). Their known occurrence ranges from Norway down to Angola in the eastern Atlantic (e.g., Colman et al., 2005; Foubert et al., 2008; Le Guilloux et al., 2009; Mortensen et al., 2001; Wheeler et al., 2007) and from North Carolina (US) to Argentina at its western side (e.g., Carranza et al., 2012; Grasmueck et al., 2006; Hebbeln et al., 2014; Mienis et al., 2014; Muñoz et al., 2012; Viana et al., 1998) and still new coral mound areas are continuously being discovered. Coral mounds occur on the shelf and along the upper to mid slope being mainly confined to water

depths of 200 to 1000 m (Roberts et al., 2009; Wienberg and Titschack, 2017). They are grouped into provinces comprising several 10s to 100s of individual mounds (e.g., Glogowski et al., 2015; Hebbeln et al., 2014; Mortensen et al., 2001), which often show a slope-parallel arrangement along distinct isobaths (Beyer et al., 2003) or are even merged to (almost) continuous belts extending over a lateral distance of 100s of kilometres (Ramos et al., 2017; Wienberg et al., 2018). The appearance of coral mounds is highly variable (circular to oval, arcuate to V-shaped, elongated to ridge-like, irregular to multi-peaked), which is often related to the prevailing current regime shaping the mounds (e.g., Correa et al., 2012; Lüdmann et al., 2016). Their dimension varies considerably with heights from a few metres to impressive values of > 300 m in height and a lateral extension from a few 10s to several 100s of metres (e.g., Mienis et al., 2007; Wheeler et al., 2007).

Coral mounds develop over geological timescales (up to millennia

* Corresponding author.

E-mail address: dhebbeln@marum.de (D. Hebbeln).

<https://doi.org/10.1016/j.margeo.2019.02.001>

Received 9 July 2018; Received in revised form 28 December 2018; Accepted 8 February 2019

Available online 11 February 2019

0025-3227/ © 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

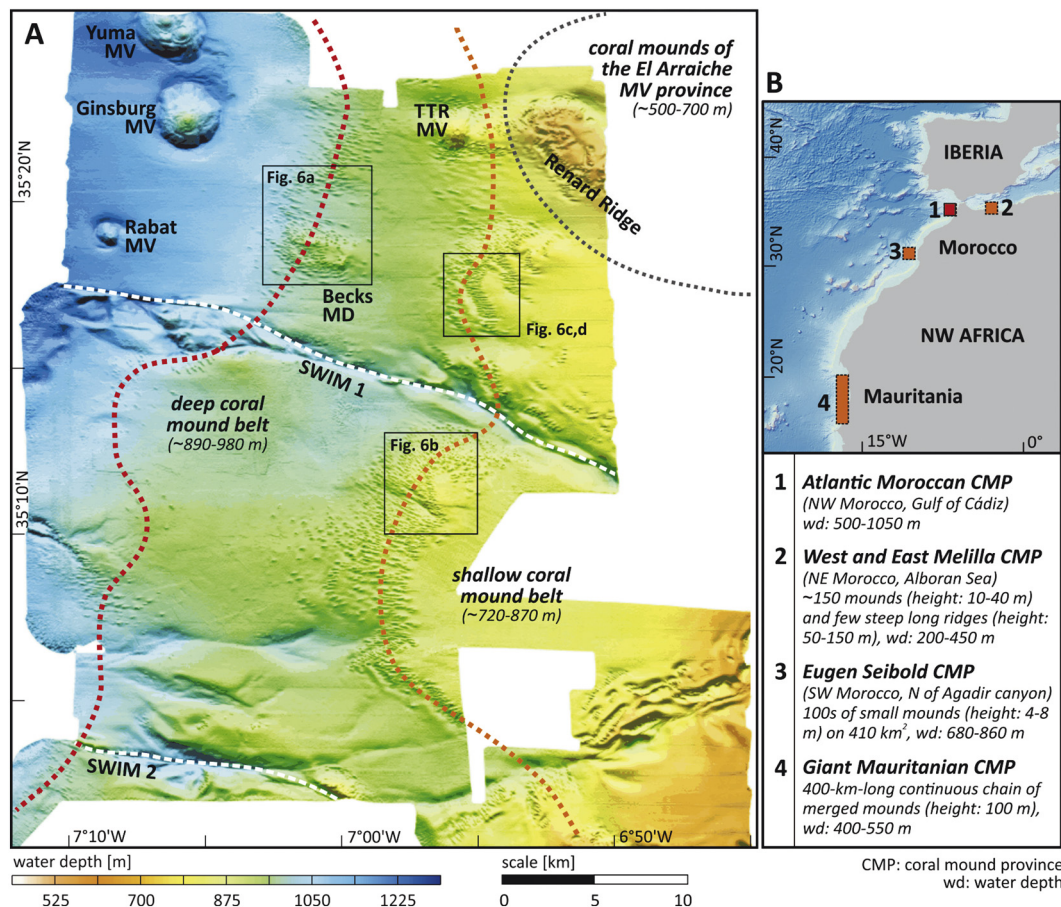


Fig. 1. (A) Bathymetric map of the Atlantic Moroccan Coral Mound Province (AMCP) off NW Morocco (indicated as site 1 in the overview map shown in B). In the NE part of the area (grey shaded), coral mounds are present within the El Arraiche mud volcano province restricted to water depths of 500–700 m (Foubert et al., 2008; Van Rooij et al., 2011). In water depths deeper than 700 m, coral mounds are mostly arranged along two slope-parallel belts, which follow distinct depth levels (shallow belt: 720–870 m, orange dotted line; deep belt: 890–980, red dotted line). In addition, several large mud volcanoes (MV), one mud diapir (MD), and two fault lines belonging to the South Western Iberian Margin (SWIM) fault system (white dashed lines) are indicated. Boxes mark location of detailed maps shown in Fig. 6. (B) Overview map of the NW African margin showing known CMPs (red/orange boxes). 1: Atlantic Moroccan CMP (red box - this study; Foubert et al., 2008; Van Rooij et al., 2011; Vadorpe et al., 2017), 2: West and East Melilla CMPs in the southern Alboran Sea (Fink et al., 2013; Hebbeln, in press; Lo Iacono et al., 2014), 3: Eugen Seibold CMP north of the Agadir canyon (Glogowski et al., 2015), 4: Giant Mauritanian CMP (Ramos et al., 2017; Wienberg et al., 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and more), resulting from the interplay of the sustained proliferation of framework-forming cold-water corals (mainly *Lophelia pertusa*) and the capability of the coral framework to baffle suspended sediments from the near-bottom waters. Both depend on vigorous and turbulent bottom current conditions to (i) secure the food supply enabling the growth of the cold-water corals (e.g., White et al., 2005), and to (ii) provide a sufficiently high, lateral supply of sediments that substantially contributes to mound aggradation (Wienberg and Titschack, 2017). Consequently, the inevitable link to bottom currents and sediment supply often places coral mounds in the direct neighbourhood of contourite drifts (Hebbeln et al., 2016). Evidenced by their elevated three-dimensional shape, coral mounds reveal higher average aggradation/sedimentation rates compared to the adjacent sea floor, even though their temporal development is often discontinuous and marked by unconformities (e.g., Eisele et al., 2008; Matos et al., 2017; Raddatz et al., 2014; Rüggeberg et al., 2007; Thierens et al., 2010; Victorero et al., 2016; Wienberg et al., 2018). Nevertheless, coral mounds represent unique sedimentary archives as they particularly aggrade under high energetic conditions, and hence, preserve sedimentary successions, which are often lacking in the surrounding area where non-deposition or erosion prevail (Thierens et al., 2013; Titschack et al., 2009).

The current knowledge about coral mounds largely originates from examples that have today an elevated and exposed position at the

seabed surface. However, coral mounds also occur as buried structures beneath the seafloor. Due to their highly heterogeneous composition (coral skeletons, other shells, fine hemipelagic sediments), the internal structure of coral mounds appears acoustically transparent and can be detected by seismic mapping (e.g., Huvenne et al., 2003). Such “buried mounds” have so far been discovered along the Irish, Moroccan and Mauritanian margins and in the Mediterranean Sea (Colman et al., 2005; Foubert et al., 2008; Huvenne et al., 2007; Lo Iacono et al., 2014), where they root either on one single horizon (Henriet et al., 1998; Huvenne et al., 2007) or originated from multiple horizons (Vadorpe et al., 2017; Lo Iacono et al., 2014).

Mound deposits comprise a substantial content of carbonate that is mainly produced by the cold-water corals and to a minor degree by their associated fauna. This carbonate (defined as “mound-derived carbonate” according to Titschack et al., 2015) can contribute up to 50 wt% to the total mound sediments (Dorschel et al., 2007a; Rüggeberg et al., 2007; Titschack et al., 2009). A first study by Lindberg and Mienert (2005) pointed out that the amount of carbonate deposited within coral mounds might play a significant role in global carbonate budgets. However, these potentially important carbonate factories are still largely neglected in any calculations (for an example see Smith and Mackenzie, 2016). This is partly ascribed to the low number of existing and locally restricted studies estimating carbonate accumulation rates

for individual coral mounds (along the Irish margin; Dorschel et al., 2007a; Rüggeberg et al., 2007; Titschack et al., 2009) or for specific regions (Mediterranean Sea, Norwegian shelf; Titschack et al., 2015, 2016). The limited amount of studies quantifying the contribution of coral mounds to the ocean carbon cycle is even more related to the facts that we are still facing an incomplete picture (i) about the worldwide distribution of coral mounds, particularly due to the rather limited availability of high-resolution bathymetric data to map exposed coral mounds and also of seismic data to detect buried mounds, and (ii) about their temporal development. Detailed studies on coral mounds describing their distribution (spatial density, alignment, water depth) and morphology (shape, dimension, orientation) within a given province are rare or lack thorough statistical analyses (Diesing and Thorsnes, 2018; Grasmueck et al., 2006; White and Dorschel, 2010). However, such knowledge will be essential to better understand the genesis and evolution of coral mounds and it will be crucial to evaluate their global importance as significant carbon sinks, their potential as unique palaeo-archives recording environmental change (e.g., Thierens et al., 2013) and their role as biodiversity hotspots in the deep sea (Henry and Roberts, 2017).

This study aims to contribute to this knowledge by introducing an extraordinary large coral mound province that has been recently discovered along the NW Moroccan Atlantic margin (Hebbeln et al., 2015; Vadorpe et al., 2017). Since the first discovery of coral mounds in the El Arraiche area (Foubert et al., 2008; Van Rooij et al., 2002), detailed mapping has continued to the southwest, where further coral mounds were detected in water depths mainly deeper than 700 m (Hebbeln et al., 2015). Here, we present a detailed bathymetric map of this deep coral mound province along the Atlantic margin off NW Morocco (35°N–35.5°N; in the following referred to as the Atlantic Moroccan coral mound province, AMCP). The new data reveal the regional dimension of coral mound distribution by documenting the presence of thousands of small- to medium-sized coral mounds within an area of 1440 km² (Fig. 1A). Using GIS analysis, the hydroacoustic data are used to analyse the quantity, dimension, shape and orientation of the exposed mounds. These data provide important information to elucidate and assess the main hydrodynamic processes (e.g., geostrophic currents, internal waves and tides) controlling the coral mound distribution and their past development.

In addition, by combining our new data on exposed mounds based on multibeam echosounder data with existing information on the presence of buried mounds observed on sub-bottom profiles (Vadorpe et al., 2017), we are able to extrapolate the total number of exposed and buried coral mounds occurring in the entire area, thus adding a third dimension (depth) to assess the actual extent in mound distribution. Finally, a first rough estimation of the total mound volume and the total (mound-derived) carbonate stored in the mounds highlights the role of the AMCP in contributing to the regional carbonate budget.

2. Study area

The Atlantic margin off NW Morocco is characterized by a complex geological history comprising several phases of rifting, compression and strike-slip motion since the Triassic (Maldonado et al., 1999; Medialdea et al., 2004). Until today, the region is influenced by the African-Eurasian plate convergence and the westward migration of the Gibraltar arc, both resulting in the emplacement of a large allochthonous wedge (Maldonado et al., 1999; Zitellini et al., 2009). On top of this unit, a Neogene sediment cover is deposited (Flinch et al., 1996), which is pierced by numerous mud volcanoes, salt diapirs, diapiric ridges and pockmarks controlled by processes associated to subsurface fluid flow and shallow gas, hydrocarbons and gas hydrates (e.g., Depreiter et al., 2005; León et al., 2012; Pinheiro et al., 2003; Somoza et al., 2003; Van Rensbergen et al., 2005; Van Rooij et al., 2005). Prominent tectonic and structural features comprise two large reactivated strike-slip faults belonging to the South Western Iberian Margin (SWIM) fault system

(Zitellini et al., 2009), many smaller faults in the subsurface (Vadorpe et al., 2017), and compressive ridges that are expressed by large rotated blocks (e.g., the Renard and Vernadsky ridges of the El Arraiche mud volcano field; Van Rensbergen et al., 2005).

The Atlantic margin between the Iberian Peninsula and the NW Morocco is well-known as a key area for the development of contourite drifts (Hernández-Molina et al., 2014). In particular, in the northern part of this region, an extensive contourite depositional system generated from the interaction of the Mediterranean Outflow Water and the slope morphology (Hernández-Molina et al., 2008). However, the southern sector off the Moroccan margin also is characterized by contourite deposition (e.g., Van Rooij et al., 2011; Vadorpe et al., 2014). These observations suggest this region as being affected by strong hydrodynamics, a preconditioning factor for cold-water coral growth. However, scleractinian cold-water corals were first reported from various mud volcanoes, where they were found as fossil accumulations on several summits (Pinheiro et al., 2003; Somoza et al., 2003).

Coral mounds were first discovered in this region in 2002 during R/V *Belgica* cruise “CADIPOR I” (Van Rooij et al., 2002), led by Jean-Pierre Henriot, one of the leading pioneers in cold-water coral research, to whom this special issue is dedicated. Detailed mapping of the so-called El Arraiche mud volcano province revealed the presence of large mud volcanoes and two prominent structural highs (Renard and Vernadsky ridges; Van Rensbergen et al., 2005). In addition, ~200 coral mounds were found to be mainly arranged on the top of and around both ridges, having heights of 15–30 m and being confined to water depths of 500–700 m (Foubert et al., 2008; Van Rooij et al., 2011). Stratigraphic studies revealed that the mounds mainly developed during deglacial and glacial periods of the Late Quaternary, while mound formation stagnated since the Holocene and remains in a dormant state until today (Frank et al., 2011; Wienberg et al., 2010). At present, the Moroccan coral mounds are covered by exposed fossil coral remains (mainly *L. pertusa*, *Madrepora oculata*, various dendrophylliid and solitary species; see Wienberg et al., 2009) lacking any coverage by fine sediments (Wienberg et al., 2009) or colonisation by living coral communities (e.g., De Mol et al., 2012).

Under present-day conditions, the depth range occupied by the coral mounds is bathed by the southward-flowing North Atlantic Central Water (NACW; ~100 to 600 m) and the northward flowing Antarctic Intermediate Water (AAIW; 600 to 1500 m) with occasional occurrences of mesoscale eddies transporting Mediterranean Outflow Water southward to this region (Machín et al., 2006; Louarn and Morin, 2011; Vadorpe et al., 2016). Along the boundary of the NACW and AAIW internal waves have been observed (Mienis et al., 2012; Vadorpe et al., 2016).

3. Data acquisition and processing

All hydroacoustic data presented in this study were collected during expedition MSM 36 (“MoccoMeBo”) with the German R/V *Maria S. Merian* in early 2014 (Hebbeln et al., 2015). Sound velocity profiles through the water column, which are essential for the correction of the hydroacoustic measurements, were repeatedly recorded using either CTD casts or sound velocity probes. To validate the nature of seabed features indicated on the obtained bathymetric map, ground-truth data were collected comprising sediment samples and video-based seafloor observations obtained during MSM 36 (Hebbeln et al., 2015) and several other expeditions (Hebbeln et al., 2008; Pfannkuche and shipboard scientific party, 2007; Van Rooij et al., 2013).

3.1. Multibeam echosounder system (MBES)

Seabed mapping was performed using a KONGSBERG EM122 multibeam echosounder system (MBES) operating at a frequency of 12 kHz covering an area of 1440 km². Operating in high-density mode, the EM122 emits 432 soundings per ping, 864 soundings in dual swath

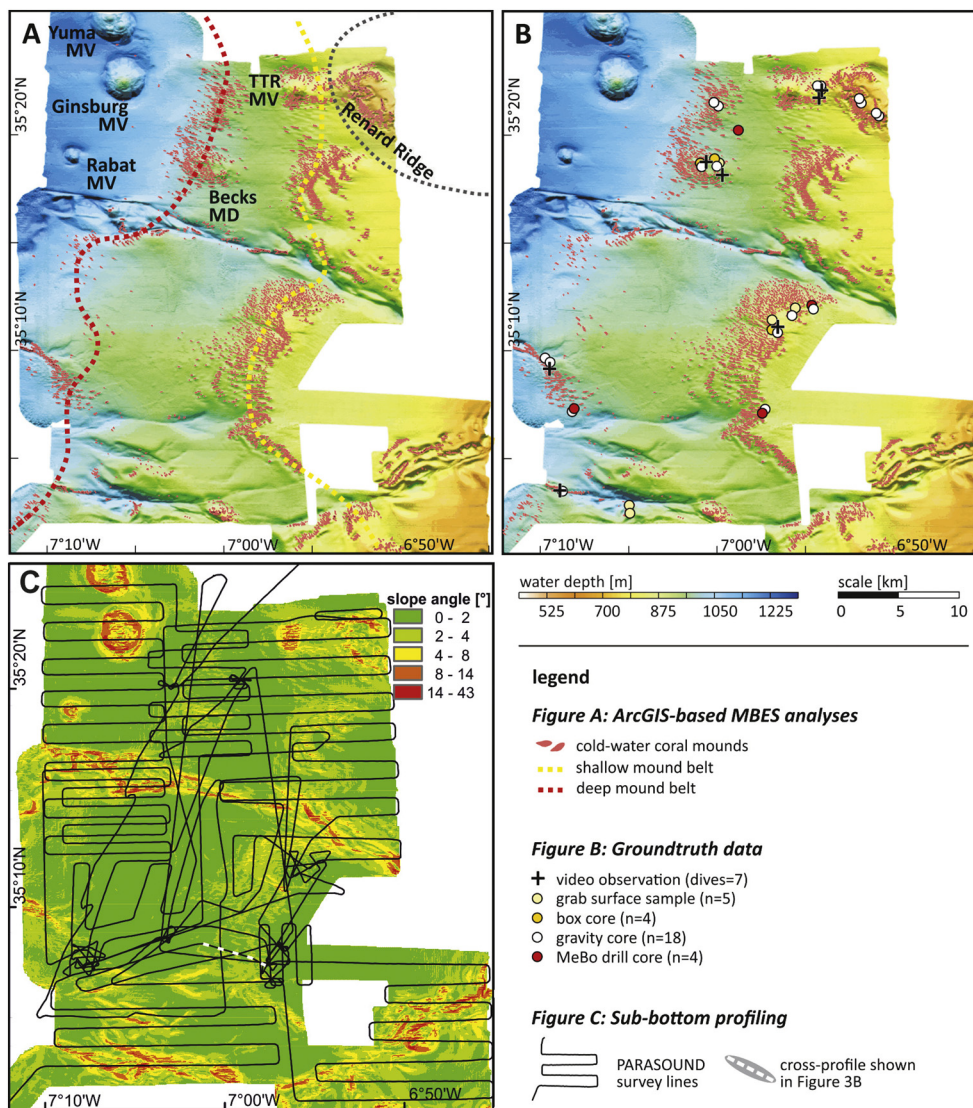


Fig. 2. (A) Overview map showing coral mounds (pink dots) in the Atlantic Moroccan Coral Mound Province (AMCP) identified by the ArcGIS™ analyses. (B) Documentation of ground-truth information (seabed samples and video observations) available from coral mounds in this area (collected during various expeditions; Hebbeln et al., 2008, 2015; Pfannkuche and shipboard scientific party, 2007; Van Rooij et al., 2013). (C) Slope angle map overlain by an overview of the PARASOUND sub-bottom survey lines used to assess the distribution of buried mounds (see Vandorpe et al., 2017). The white dashed line indicates the position of a cross profile shown in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mode while covering a swath width of 120°. On a flat seafloor, the coverage is equal to 3.5 times the water depth. The vertical resolution depends on the pulse length that depending on the water depth was chosen automatically. Spatial integrity of the mapping data were achieved by combining the ship's SEAPATH 200 inertial navigation system (INS) including differential global positioning system (DGPS) information with attitude data (roll, pitch, heave) provided by the motion reference unit (MRU) 5+. The open-source software package MB-System v.5.3.1 (Caress and Chayes, 1996) and the Generic Mapping Tool (GMT) v.4.3.1 (Wessel and Smith, 1998) were used for bathymetric data processing, editing and quality control. ESRI ArcGIS™ v.10 was used to create maps (grid cell size: 10 m), a spatial data management and for GIS analyses. In addition, the polygon-feature layer which shows the extracted CWC mounds (see below) has been utilized to subtract the CWC areas from the original DTM with a 10 m grid cell size. An interpolation and a resampling then provides a 50 m DTM from which a slope angle map is derived to illuminate general slope morphology.

3.2. GIS analyses

The huge amount of coral mounds visible in the bathymetric data (Fig. 1) required a standardized approach to quantify the individual coral mounds. We therefore utilized the Bathymetric Positioning Index

(BPI), the marine version of the topographic position index (TPI), introduced by Weiss (2001). The BPI algorithm is part of the *Benthic Terrain Modeler* (BTM), an ArcGIS™ add-on toolbox developed by Wright et al. (2005). The BPI expresses the comparison of elevation of each cell in the bathymetric grid with the elevation of a defined neighbourhood around that cell, thus, putting each cell into its local context. As stated in Erdey-Heydorn (2008), using such a tool is an iterative process (trial and error) as there is no defined special method to set the most suitable inner and outer radii for the neighbourhood when targeting specific subjects, as e.g. coral mounds. Thus, we conducted manual measurements on 64 coral mounds to retrieve the inner and outer radii demanded for the BPI raster calculations. The selected 64 mounds are representative for all kind of mound shapes and sizes detected in the mapped area. Their length, width and height were measured to get an overview of the expected dimensions. Finally, an inner radius of $1 \times$ and an outer radius of $9 \times$ the grid cell size (10 m) were adopted to isolate the mound features. The resulting BPI raster data set allowed to classify ridges, peaks, depressions, slopes, and plains (Wright et al., 2005), with the ridges corresponding to coral mounds. Based on this classification, polygons defining the ridges were created in ArcGIS™ and the bounding rectangles provided the length and width of all detected mounds. To provide a conservative estimate of the basal area (i.e., the footprint) of the mounds, we assumed their shape to be close to an ellipsoid and used following equation for calculation: basal

area = 0.5 length \times 0.5 width \times π . The two ArcGIS™ tools *Minimum Bounding Geometry* and *Calculate Polygon Main Angle* were used to define the orientation of the mounds by defining the main direction of all polygons having a well-defined length axis. A threshold for the length-to-width ratio of 1.3 was used, to differentiate between round to oval (< 1.3) and elongated (\geq 1.3) mound shapes.

4. Results

4.1. Multibeam bathymetry and GIS analyses

The multibeam bathymetric mapping covered an area of 1440 km² along the NW Moroccan Atlantic margin. Most prominent features within the mapped area (Fig. 1A) are four mud volcanoes (Yuma, Ginsburg, TTR, and Rabat; Pinheiro et al., 2003; Somoza et al., 2003), the Becks mud diapir (León et al., 2012), the Renard Ridge (Van Rensbergen et al., 2005), and two major NW-SE-trending fault lines being related to the SWIM fault system (Vandorpe et al., 2017; Zitellini et al., 2009). In addition, the detailed bathymetry map reveals a large number of rather small elevated features (Fig. 2a). These features were proven to represent coral mounds through the collection of groundtruth data (see Fig. 2B) during various expeditions comprising grab surface samples ($n = 5$), sediment cores (box cores, gravity cores, and drill cores obtained with the Bremen seafloor drill rig MeBo; $n = 26$) and video footage (ROV, camera sledge; $n = 7$). All collected sediment material showed a typical coral mound facies characterized by varying but generally high contents of coral fragments embedded in a matrix of hemipelagic sediments. The video surveys crossing many of the mound structures revealed that the mounds' surfaces are densely covered by coral rubble and dead coral framework (Fig. 3A), whereas living scleractinian corals are extremely rare today (for details on the sampling and video observations see the respective cruise reports; Hebbeln et al., 2008, 2015; Pfannkuche and shipboard scientific party, 2007; Van Rooij et al., 2013). In addition, geophysical data obtained from the area (1430 km of PARASOUND sub-bottom profiles shown in Fig. 2C) showed the presence of exposed and buried coral mounds (Vandorpe et al., 2017) indicated by their acoustic transparency (Fig. 3B).

The ArcGIS™-based analyses revealed a total of 3463 coral mounds within the mapped area of the AMCP (Fig. 2A) that result in a mound density of 2.4 mounds per km². Overall, the mounds occur in water depths ranging from 565 m to 1155 m (Fig. 4A). However, they are largely confined to two slope-parallel belts extending along the continental slope (Figs. 1, 2A). Defined by > 80 mounds per 10 m depth interval (> 50 mounds for the area between the two mound belts), the deep belt of coral mounds is centred between 890 m and 980 m water depth. It comprises about 24% ($n = 827$) of all mounds (Fig. 4A). The shallow mound belt is largely confined to a water depth range of 720 m to 870 m. The majority of mounds (59%, $n = 2057$) is arranged within this belt (Fig. 4A). Across the mound belts the slope is slightly steeper (2–3°) than across the area between the two mound belts (< 1°, 870–890 m water depth) (Fig. 1C) that hosts only a few mound

structures (< 4%). Also below (> 980 m) and above (< 720 m) the two mound belts, only a rather low number of mounds was detected (< 4% and 10%, respectively).

The coral mounds have lengths ranging from 24 m to 2075 m (mean: 186 m, Standard Deviation (SD) 149 m; Fig. 4C). Their width ranges from 12 m to 584 m (mean: 77 m, SD 41 m; Fig. 4D). Information on the height of the mounds only exists for the 64 mounds that were individually measured for their dimensions to scale the radii for the BTM. These mounds range in height from 4 m to 50 m above the current seafloor with a mean of 18 m (SD 11 m). The individual mounds are estimated to cover areas of 300 m² to 950,000 m² (mean: 14,500 m²; SD 27,075 m²; Figs. 4E, 5B), although only 20 out of 3463 mounds have basal areas larger than 120,000 m².

As indicated by the considerably higher average length compared to the average width of the mounds, reaching peak length-to-width ratios of > 10, the majority of all mounds reveal an elongated morphology, with only 15% of all mounds having a round to oval shape with a length-to-width ratio of < 1.3 (Fig. 5C). There is no relation between the degree of elongation and mound height. The elongated mounds have a predominant extension of their length axis in ESE-WNW direction (Figs. 4B, 5A), i.e. they are mostly extended downslope rather than parallel to the continental slope. Interestingly, neither the size and shape nor the orientation of the mounds shows any relation to water depth (Fig. 5).

5. Discussion

5.1. Quantification of coral mounds

The GIS-based evaluation of the multibeam bathymetry data revealed a total of ~3400 coral mounds distributed over an area of 1440 km² resulting in an average density of 2.4 mounds/km². However, there is quite a variability in the density of the mounds, in particular, as the mounds of the AMCP are mainly concentrated in two sub-parallel belts (Figs. 1, 4A). Thus, on smaller scales, mound densities can reach even > 10 mounds/km² (see also Fig. 6). Such mound densities are close to observations from the Mediterranean Sea, where ~3–5 mounds/km² were observed (Lo Iacono et al., 2014; Savini and Corselli, 2010), and from the southern Moroccan margin, where 2–12 mounds/km² were found (Glogowski et al., 2015). For most other coral mound regions, such quantifications are missing. Nevertheless, the high number of mounds often found in individual coral mound provinces (e.g., Hebbeln et al., 2014; Muñoz et al., 2012; White and Dorschel, 2010) as well as the continuous discovery of new provinces – at least around the Atlantic – point to their role as common seabed features usually occurring in intermediate water depths that up to date have been largely neglected in any classification schemes describing submarine landscapes (e.g., Greene et al., 1999).

While buried coral mounds are occasionally reported from coral mound provinces in the NE Atlantic and the Mediterranean Sea (Colman et al., 2005; Henriot et al., 1998; Lo Iacono et al., 2014),

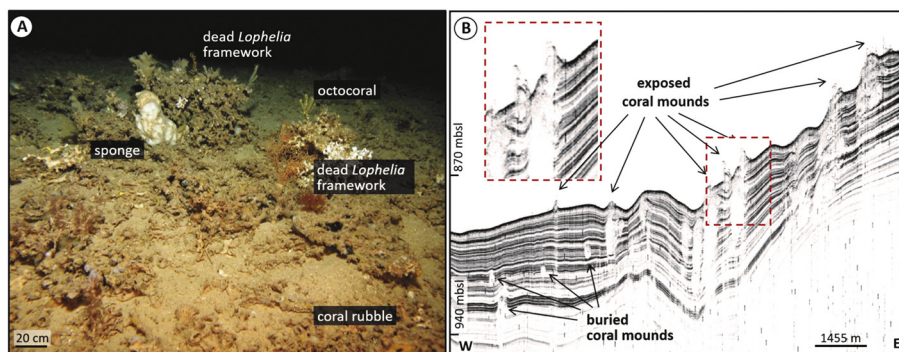


Fig. 3. (A) Still photograph showing the surface of a coral mound of the Atlantic Moroccan Coral Mound Province (AMCP) taken by the ROV Cherokee during R/V Pelagia cruise 64PE284 (Hebbeln et al., 2008). The surface of this mound is covered by dead/fossil coral framework. (B) PARASOUND sub-bottom profile showing exposed and buried coral mounds of the AMCP. The mounds root on multiple horizons pointing to several mound formation periods during the past (see also Vandorpe et al., 2017). The small box highlights the reflection pattern associated with selected coral mounds. The position of the profile is indicated in Fig. 2C.

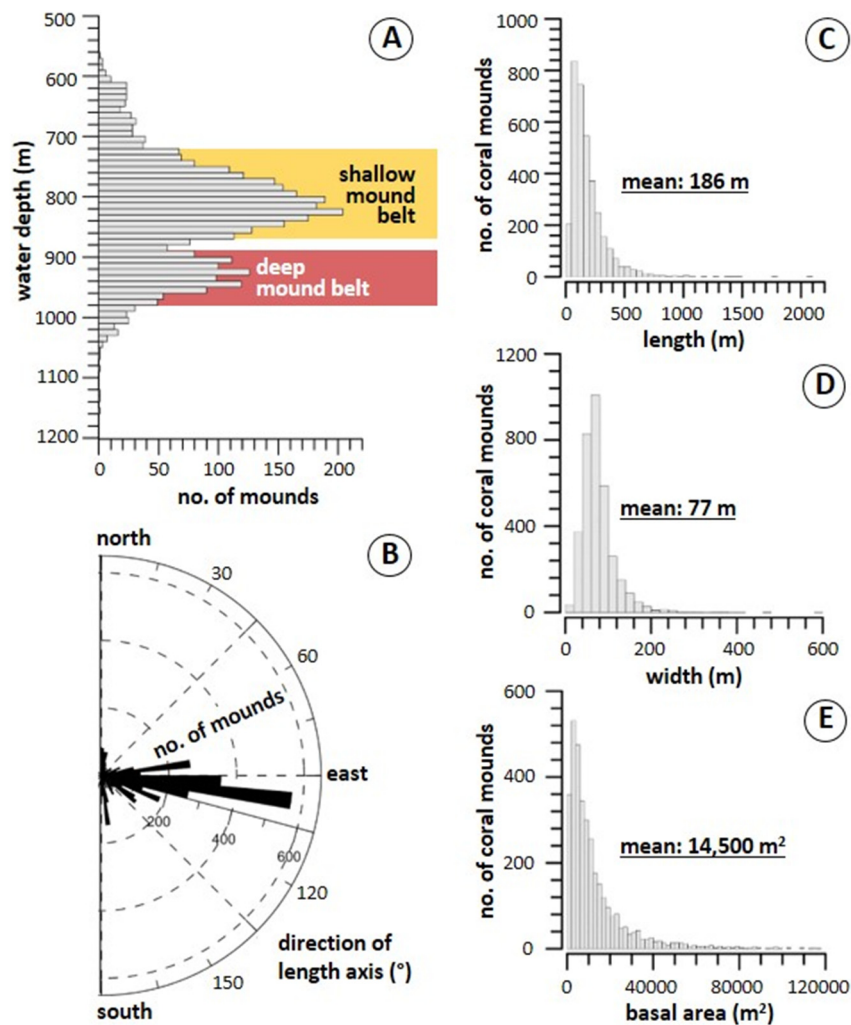


Fig. 4. Spatial distribution and morphometric data analysed for 3463 coral mounds that were identified on an area of 1440 km² along the NW Moroccan Atlantic margin. (A) Water depth versus coral mound distribution highlighting the two maxima (marked by yellow and red shaded bars, respectively) related to the two mound belts shown in Fig. 1. (B) Pre-dominant directions of the length axes of the mounds. Histograms showing (C) the length and (D) the widths of the mounds, and (E) the basal area covered by the mounds (here those 20 out of 3463 mounds having basal areas between 120,000 m² and 950,000 m² are not shown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detailed or even quantitative studies of buried mound occurrences are rare (Huvenne et al., 2003). However, buried mounds that are present in the AMCP were quantified based on the analysis of hydroacoustic sub-bottom profiles (PARASOUND: ~1430 km; single channel reflection seismic sparker: ~650 km; Vandorpe et al., 2017) revealing a total of 781 mounds that root on ten different horizons within the upper 150 m of the seafloor (according to the maximum penetration depth of the acoustic devices; Vandorpe et al., 2017). Along these profiles, only 166 mounds pierce the seafloor, while 615 mounds are completely buried resulting in a buried vs. exposed mound ratio of 3.7 : 1 (Vandorpe et al., 2017). By applying this ratio to the total number of ~3400 exposed mounds detected by the multibeam bathymetry data, the presence of > 12,500 buried mounds is expected for the entire area. Thus, adding the ~3400 exposed mounds, an impressively high number of ~16,000 buried and exposed mounds is estimated for the AMCP (Fig. 1).

The extraordinary high number of coral mounds in the AMCP comprising multiple generations of coral mounds (Vandorpe et al., 2017) provide important information on the dynamics of coral mound formation. Obviously, this can be much more variable than previously assumed as recently outlined by Wienberg et al. (2018), who identified distinct temporal differences in mound formation stages even for directly neighbouring coral mounds within the Mauritanian cold-water coral province. It appears that already small differences in the environmental factors impacting on neighbouring coral mounds decide on their fate, namely whether they become buried or re-start their aggradation during the following phase of favourable conditions for coral

growth (Vandorpe et al., 2017). This variable response combined with a dynamic paleo-environmental setting creates a diversity in individual mound histories that has never been described before.

5.2. Distribution and orientation of coral mounds – controlled by internal waves?

With ~25% of all mounds occurring deeper than 900 m, the coral mounds of the AMCP are among the deepest coral mounds described so far. The only other examples of such deep coral mound occurrence exist along the Irish (White and Dorschel, 2010) and the Scottish margin (Masson et al., 2003; Huvenne et al., 2009). A peculiar observation from the AMCP is the arrangement of the coral mounds in two slope-parallel mound belts with an average depth offset of ~140 m (Figs. 1, 4A). Interestingly, similar patterns were also observed off Ireland, where two mound belts occur between ~800 and 1000 m water depth (Beyer et al., 2003), and off Mauritania, where mounds are arranged in two slope-parallel (almost) continuous chains in 400 and 550 m water depth (Wienberg et al., 2018). The rather similar depth offset of 140–200 m between the mound belts is in the order of glacial-interglacial sea level variations (Grant et al., 2014), and thus, might point to different vitality phases of upper and lower mound belts in pace with such climate-driven sea level changes. However, independent of the depth of the mound belts, coral mound formation was off Ireland limited to interglacial periods, while mound formation off Morocco was mainly restricted to glacial periods (Frank et al., 2011; Wienberg et al., 2010). Considering these temporal restrictions of mound formation in

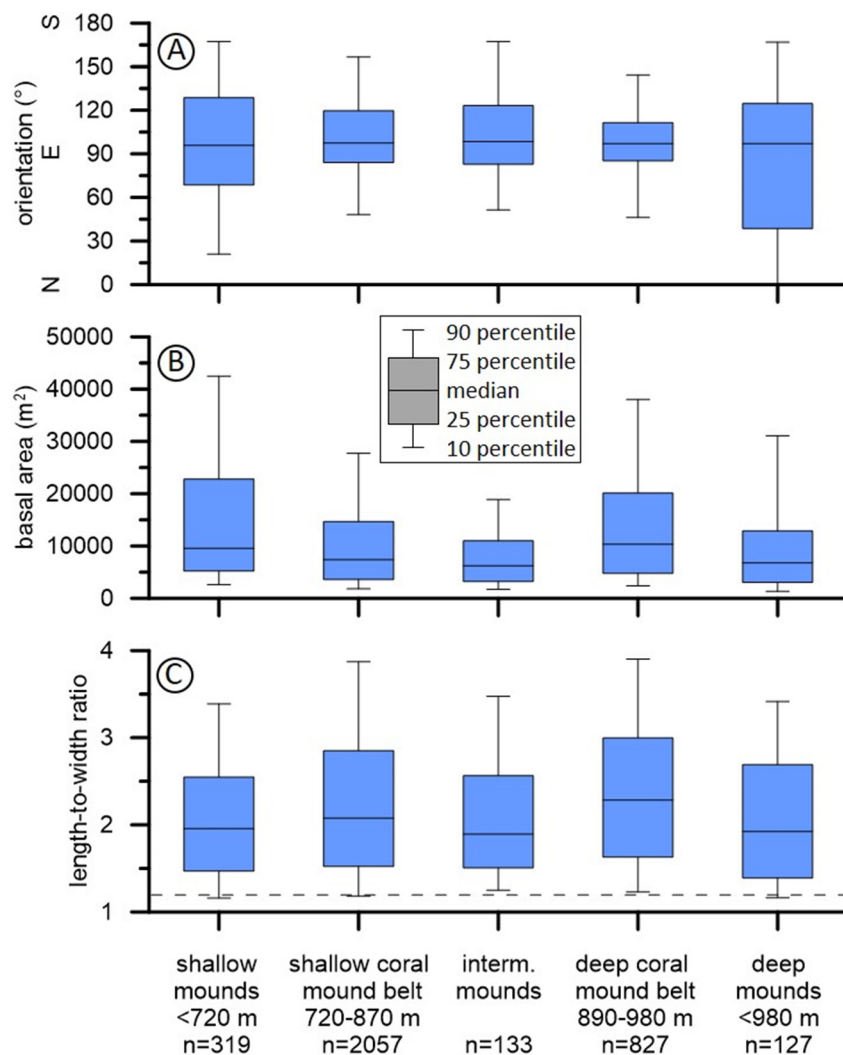


Fig. 5. Box-whisker plot (displaying the 90/10 percentile at the whiskers, the 75/25 percentiles at the boxes, and the median in the centre line) of morphometric data obtained for coral mounds of the Atlantic Moroccan Coral Mound Province (AMCP). The data for the 3463 mounds are differentiated according to water depth with most of the mounds belonging to the two major mound belts described in the text. (A) Orientation of the longest mound axes. (B) Basal area of the mounds. (C) Length-to-width ratio describing the degree of elongation of the mounds. The dashed line represents the threshold value of 1.3 used to differentiate between round and elongated mounds.

the specific regions, large-scale climate change-driven sea level variability cannot be the factor controlling the depth offset between the coral mound belts. Also off Mauritania, where the history of coral mound development is more complex, a glacial-interglacial-driven switching of mound aggradation among the upper or lower mound belts can be excluded (Wienberg et al., 2018).

Although the slope-parallel extension of the coral mound belts in the AMCP might imply a link to the prevailing oceanographic current system, a closer look at the shape and orientation of the individual mounds points to a different forcing factor. Elongated mound shapes, dominating the study area (85%) over the entire investigated depth range (Fig. 5C), are commonly interpreted as current-induced with the length axes paralleling the main current direction by stimulating coral growth predominantly towards the approaching current, i.e. towards the delivery of food particles (Correa et al., 2012; Lüdmann et al., 2016; Messing et al., 1990; Mienis et al., 2014). Interestingly, in the AMCP the length axes of the mounds generally have a predominant E-W direction, i.e. downslope or across-slope and, thus, perpendicular to the direction of the main currents (Fig. 4B), irrespective of the depth level (Fig. 5). However, close inspections of the bathymetric data reveal clear evidence for a dominant local-scale hydrodynamic control of the shape of many of the mounds, where seafloor complexity has a primary role in defining the distribution patterns of bottom currents. For instance, several mounds are aligned around the Becks mud diapir (northern part of the deep mound belt; Fig. 1A) and show orientations clearly driven by slope-perpendicular flow streaming around the larger elevation

created by the mud diapir (Fig. 6A).

In the southern part of the shallow mound belt (Fig. 1A), a distinct promontory is covered by a radial pattern of elongated mounds that are always directed downslope, although at this site the mounds are only slightly elongated (Fig. 6B). Further north, down-slope directed elongated mounds open into a little slope-parallel valley that can be interpreted as a plunge pool to which downslope transport of turbid waters passing between the mounds deliver sediments forming the western wall of the plunge pool (Fig. 6C, D). In addition, the straight, ridge-like shape of these mounds with steep flanks and deep moats developed between the mounds points to high energetic down/up-slope orientated hydrodynamics.

All these observations clearly point to a predominant influence of hydrodynamic processes acting in downslope/upslope directions from the shallowest to the deepest mounds (Fig. 5) also crossing the main regional water mass boundary between the NACW and the AAIW at around 600 m water depth (with a mixing zone between both water masses; Louarn and Morin, 2011). While these water masses are mainly transported northward/southward along the slope, additional E-W oriented currents were observed close to the sea floor (Vandorpe et al., 2016). Field measurements identified these currents to be related to the effect of internal tides (Vandorpe et al., 2016) that commonly act perpendicular to the slope (Pomar et al., 2012). Nearby measurements revealed maximum current speeds of $> 30 \text{ cm s}^{-1}$ and internal wave heights of up to 100 m (Mienis et al., 2012). Overall, these measures fit well to the common range of internal wave dimensions (Pomar et al.,

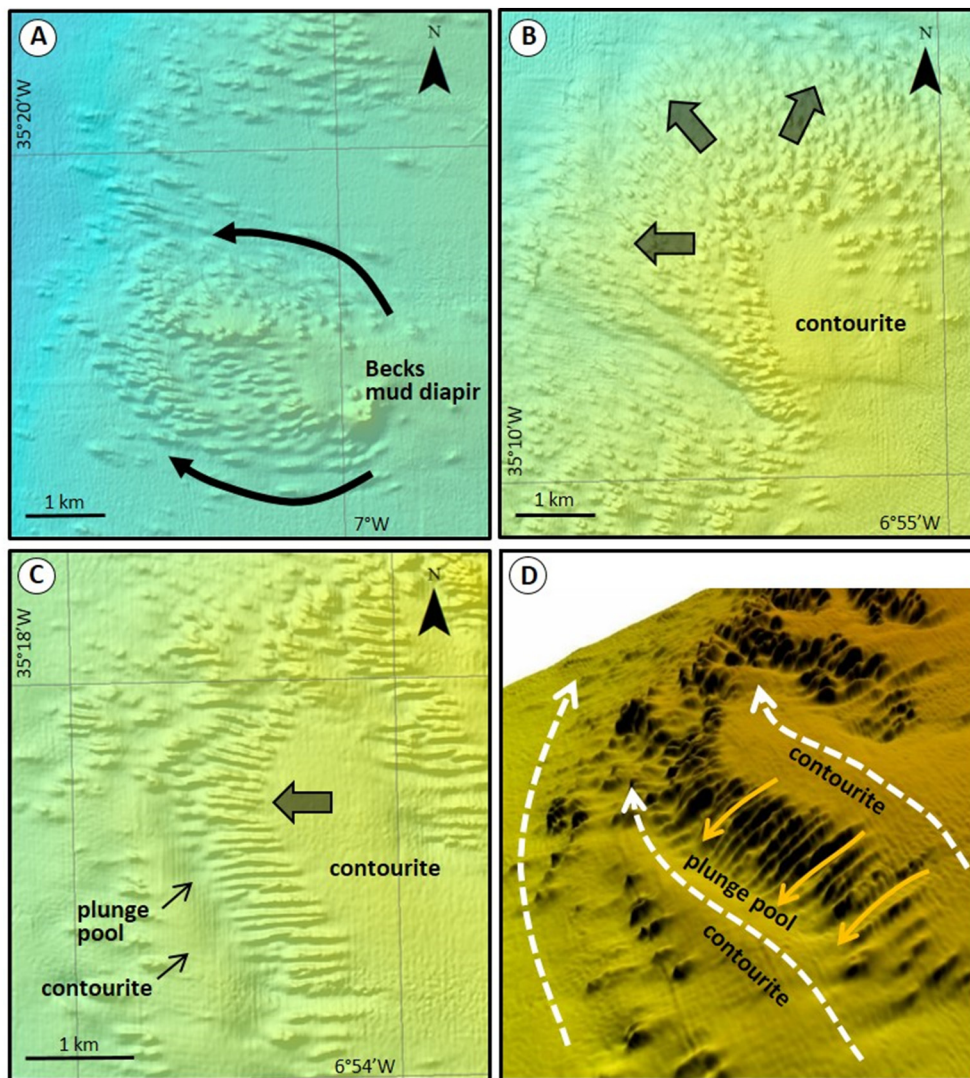


Fig. 6. Close-ups of selected coral mounds in the Atlantic Moroccan Coral Mound Province (AMCP), locations are indicated in Fig. 1. (A) Example from the northern part of the deep mound belt, showing oval to elongated coral mounds aligned around the Becks mud diapir. (B) Example from the southern part of the shallow mound belt showing a high density of circular to oval coral mounds extending radially from a large promontory. (C) Elongated, ridge-like coral mounds, which are mainly found in the northern part of the shallow mound belt. These mounds have an E-W orientation perpendicular to the slope and stretch straight downslope. (D) A 3D-view of the mounds shown in (C). Slope-parallel bottom currents (white dashed arrows) might have placed the mounds to distinct depth terraces made up by contouritic sediments. In addition, downslope currents (orange arrows) induced by internal waves possibly triggered (i) the straight elongated shape and steep flanks of these mounds as well as the deep and pronounced moats developed between them, and (ii) created a plunge pool at the base of the mounds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2012). Of course, these observations describe the present-day setting, under which the coral mounds are not active. However, assuming a similar geomorphological/hydrodynamic setting for glacial times, when CWC were actually living in this region, marked by a water mass boundary impinging on a sloping surface, a setting typical for the formation of internal waves (Pomar et al., 2012), most likely such internal waves also interacted with the active coral mounds under glacial conditions.

Internal waves and tides indeed can play an important role for cold-water corals, and hence mound formation, by enhancing the lateral transport or accumulation of particulate organic material (nepheloid layers), consequently providing an important source of food for the corals (Mienis et al., 2007) and of sediments for the formation of the coral mounds (e.g., Wienberg and Titschack, 2017). The positive feedback of internal waves on mound formation has been documented for various modern coral mound settings in the Atlantic (Davies et al., 2009; Dorschel et al., 2007b; Frederiksen et al., 1992; Hebbeln et al., 2014; Mienis et al., 2007; White and Dorschel, 2010; White et al., 2005). Palaeoceanographic changes disconnecting internal waves from coral mounds were recently claimed to cause a temporal stagnation in mound formation within the Gulf of Mexico (Campeche coral mound province; Matos et al., 2017). Thus, the slope-perpendicular orientation of the mounds in the AMCP might also be induced by the effect of internal waves that regularly release their energy along the same direction. The absence of thriving corals in the AMCP in the Holocene has

been explained by a significant decrease in surface water productivity (Wienberg et al., 2010). Thus, even the continuous presence of internal waves in the region (until) today seemingly cannot compensate the resulting lack of food.

5.3. Mound volumes and their impact on the regional carbonate budget

The volume of a coral mound is difficult to assess due to its irregular shape and its (potential) sub-seafloor extension. The resulting high natural size variability of the coral mounds in the region (see Section 4.1) precludes a detailed analysis of uncertainties and a subsequent error propagation analyses when estimating coral mound volumes. However, to get a conservative estimate of these volumes, an ellipsoidal cone (volume = $1/3 \times \text{height} \times \text{basal area}$) was assumed and the sub-seafloor mound volume was ignored. Using the mean height of 18 m and the mean basal area of 14,000 m², the average mound volume can be estimated to 84,000 m³. This number is considerably higher (2.3 times) than the average volume of 36,000 m³ presented by Vandorpe et al. (2017), though these authors used a very similar average mound height of 20 m for their estimation. Interestingly, their estimated mound height of ~20 m remained rather constant over the multiple generations of buried coral mounds reflected in the hydroacoustic data. Consequently, this number can also be used to assess the height of the multiple generations of buried mounds in the AMCP. The higher estimated mound volume of 84,000 m³ presented in this study probably

results from considering the mostly elongated shape of the mounds that is hard to extract from the 2D data of the sub-bottom profiles used by [Vandorpe et al. \(2017\)](#). Applying the estimated volume of 84,000 m³ to the number of ~16,000 mounds, the total coral mound volume within the AMCP can be roughly estimated to ~1344 km³, consisting to a large part of carbonate produced by cold-water corals.

The carbonate accumulation rates of the benthic, aphotic coral mound carbonate factory were recently described to be close to the range of tropical shallow-water coral reefs ([Titschack et al., 2016](#)). The composition of coral mounds exhibits varying contents of (i) mound-derived carbonate (mainly aragonite and high magnesium calcite) produced by the corals and other benthic organisms (such as molluscs, bryozoans, echinoderms), (ii) background carbonate (mainly low-magnesium calcite) predominantly consisting of foraminifers and coccolithophores, and (iii) siliciclastic sediments (for detailed description see [Titschack et al., 2016](#)). Based on case studies obtained from Norwegian and Mediterranean coral mounds, the average coral content stored in mound sequences can be estimated to ~20 vol% (site specific averages range between 8 vol% and 28 vol%; [Titschack et al., 2015, 2016](#)). Using a density of ~2.66 g cm⁻³ for aragonitic corals ([Dorschel et al., 2007a](#)) and a matrix sediment density of ~1.52 g cm⁻³ ([Hamilton, 1976](#)), and considering a ratio of 20 vol% : 80 vol% for corals and matrix sediments, respectively, the average density of the coral mound sediments amounts to ~1.75 g cm⁻³. Based on these assumptions, the total mound mass is estimated to be 2.3 billion tons. Assuming to account for 30 wt% ([Titschack et al., 2009, 2015, 2016](#)) the mound-derived carbonate within the coral mounds is estimated) to be 700 million tons. As this amount would be equivalent to 84 million tons of carbon, the coral mounds of the AMCP can be defined as an important carbon sink. These numbers have to be seen as a surplus adding to the carbonate accumulating as part of the common (hemi) pelagic sedimentation and, thus, represent a significant contribution to the regional carbonate budget.

To assess the importance of this contribution, it is necessary to put it into a temporal context. Using the regional seismic stratigraphy, [Vandorpe et al. \(2017\)](#) provided a rough estimate of an age of ~900 kyr for the initiation of coral mound development in the AMCP. However, as coral mound formation along the NW Moroccan margin was generally restricted to glacial periods ([Frank et al., 2011; Wienberg et al., 2010](#)), the actual time span of active mound formation is expected to be much lower and is probably in the order of ~50% of the 900 kyr time interval. Thus, deposited over ~450 kyr, the overall 700 million tons of mound-derived carbonate estimated for the AMCP would have accumulated with a mean rate of ~1550 t yr⁻¹ equalling 15.5 × 10⁶ mol carbonate yr⁻¹. According to [Milliman \(1993\)](#), the world's continental slopes (100 m to 2000 m depth interval) cover an area of 32 × 10⁶ km² with an overall accumulation of 4 × 10¹² mol carbonate yr⁻¹. With regard to the modern coral mound area within the study region, the mound-derived carbonate accumulation within the AMCP is about 2.5 times higher than the continental slope average as described by [Milliman \(1993\)](#). The pelagic carbonate production, the main contributor to the average carbonate accumulation along the continental slopes, of course, is also deposited on the coral mounds, thus, adding to the accumulation of mound-derived carbonate. Furthermore, even when corals occur over extended time spans, mound aggradation often has been described as episodic or pulsed, with short periods (i.e. several centuries) of extreme high mound aggradation of 4 m to even 16 m kyr⁻¹ ([Fink et al., 2013; Titschack et al., 2015; Wienberg et al., 2018](#)). During such fast aggradation periods, the carbonate burial can reach very high rates of 500 g cm⁻² kyr⁻¹ to even > 1000 g cm⁻² kyr⁻¹, as e.g., described for coral mounds off Norway and in the Mediterranean ([Titschack et al., 2015, 2016](#)). Applying the approach outlined above to measured glacial mound aggradation rates of 15 cm kyr⁻¹ in the AMCP ([Wienberg and Titschack, 2017](#)), mound-derived carbonate accumulated with a rate of ~80 g m⁻² yr⁻¹, which converts to a carbon sink of almost

10 g m⁻² yr⁻¹. For maximum short-term (centennial scale) accumulation rates of mound-derived carbon of > ~10,000 g m⁻² yr⁻¹ off Norway ([Titschack et al., 2015](#)) the carbon sink rates would even amount to 1200 g m⁻² yr⁻¹. Comparing this number to average carbon sink rates in boreal peatlands (~20 g m⁻² yr⁻¹; [Turunen et al., 2002](#)) or boreal forests (~44 g m⁻² yr⁻¹; [Pan et al., 2011](#)) clearly highlights the potential importance of coral mounds for regional or even global carbon budgets, especially in times of fast mound aggradation.

6. Conclusions

The NW Atlantic Moroccan margin hosts an impressive coral mound province displaying > 3400 mounds exposed at the seabed that are accompanied by an estimated 12,500 buried mounds. The exposed mounds are predominantly arranged from north to south in two slope-parallel belts. However, their mostly elongated shape with an E-W orientation perpendicular to the slope, points to strong upslope/down-slope directed hydrodynamics probably induced by internal waves controlling the mounds. An order of magnitude estimate of the mound-derived carbonate (i.e. largely produced by the cold-water corals) stored in these mounds amounts to 0.7 billion tons corresponding to 80 million tons of carbon. These amounts have been accumulated in addition to the common pelagic and benthic carbonate production and, thus, highlight the importance of cold-water coral mounds for the regional carbonate budget. A rough estimate of the accumulation rate of mound-derived carbonate yields a value of ~1550 t yr⁻¹, however, this value has to be taken cautiously until more detailed stratigraphic studies of the AMCP coral mounds become available.

Of course, the area of 1440 km² considered here is too small to allow for any upscaling to larger scales. However, the significance of these observations is highlighted by additional coral mound occurrences described from the Moroccan margin ([Fig. 1B](#)): (i) approximately 200 coral mounds occurring in the El Arraiche area directly to the north of the AMCP ([Foubert et al., 2008; Van Rooij et al., 2011; Vandorpe et al., 2017](#)), (ii) > 1000 mounds making up the so-called Eugen Seibold coral mounds north of the Agadir Canyon ([Glogowski et al., 2015](#)), and (iii) coral mounds forming the West Melilla ([Lo Iacono et al., 2014](#)) and the East Melilla ([Fink et al., 2013; Hebbeln, in press](#)) coral mound provinces along northern Moroccan margin facing the Mediterranean (Alboran) Sea. All these observations underline the role of the Moroccan margin as a hotspot area for the occurrence of cold-water coral mounds (cf., [Henriet et al., 2014](#)).

With respect to the knowledge gained over the last decade corresponding to just a very few dedicated surveys during which thousands of mounds have been detected, it is very likely that coral mounds will also be discovered at many more sites along the NW African margin (and beyond) by high-resolution bathymetric mapping in the coming years. This study adds to the cumulating evidence of a widespread presence of coral mounds – at least – along the margins of the Atlantic Ocean and highlights their potential to act as significant carbonate (and carbon) sinks.

Acknowledgements

We like to thank the nautical and scientific crews for on-board assistance during R/V *Maria S. Merian* cruise MSM36. We are also grateful for numerous very valuable comments provided by the two reviewers, Veerle Huvenne and Claudio Lo Iacono, which helped to considerably improve this manuscript. The research leading to these results has received support from the Deutsche Forschungsgemeinschaft (DFG) through providing ship time and through funding the project “MoccAMeBo” (grant HE 3412/18). This work was further supported through the DFG Research Center/Cluster of Excellence, The Ocean in the Earth System (EXC 309). The data reported in this paper are archived in Pangaea (www.pangaea.de).

References

- Beyer, A., Schenke, H.W., Klenke, M., Niederjaser, F., 2003. High resolution bathymetry of the eastern slope of the Porcupine Seabight. *Mar. Geol.* 198, 27–54.
- Caress, D.W., Chayes, D.N., 1996. Improved processing of Hydrosweep DS multibeam data on the R/V Maurice Ewing. *Mar. Geophys. Res.* 18, 631–650.
- Carranza, A., Recio, A.M., Kitahara, M., Scarabino, F., Ortega, L., López, G., Franco-Fraguas, P., De Mello, C., Acosta, J., Fontan, A., 2012. Deep-water coral reefs from the Uruguayan outer shelf and slope. *Mar. Biodivers.* 42, 411–414.
- Colman, J.G., Gordon, D.M., Lane, A.P., Forde, M.J., Fitzpatrick, J., 2005. Carbonate mounds off Mauritania, northwest Africa: status of deep-water corals and implications for management of fishing and oil exploration activities. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer, Heidelberg, pp. 417–441.
- Correa, T.B.S., Eberli, G.P., Grasmueck, M., Reed, J.K., Correa, A.M.S., 2012. Genesis and morphology of cold-water coral ridges in a unidirectional current regime. *Mar. Geol.* 326–328, 14–27.
- Davies, A.J., Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., van Haren, H., Roberts, J.M., 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef Complex. *Limnol. Oceanogr.* 54, 620–629.
- De Mol, L., Hilário, A., Van Rooij, D., Henriët, J.-P., 2012. Habitat mapping of a cold-water coral mound on Pen Duick Escarpment (Gulf of Cádiz). In: Harris, P.T., Baker, E.K. (Eds.), *Seafloor Geomorphology as Benthic Habitat*. Elsevier, London, pp. 645–654.
- Depreiter, D., Poort, J., Van Rensbergen, P., Henriët, J.-P., 2005. Geophysical evidence of gas hydrates in shallow submarine mud volcanoes on the Moroccan Margin. *J. Geophys. Res.* 110. <https://doi.org/10.1029/2005JB003622>.
- Diesing, M., Thorsnes, T., 2018. Mapping of cold-water coral carbonate mounds based on geomorphometric features: an object-based approach. *Geosciences* 8, 34.
- Dorschel, B., Hebbeln, D., Rüggeberg, A., Dullo, C., 2007a. Carbonate budget of a cold-water coral carbonate mound: Propeller Mound, Porcupine Seabight. *Int. J. Earth Sci.* 96, 73–83.
- Dorschel, B., Hebbeln, D., Foubert, A., White, M., Wheeler, A., 2007b. Hydrodynamics and cold-water coral facies distribution related to recent sedimentary processes at Galway Mound west of Ireland. *Mar. Geol.* 244, 184–195.
- Eisele, M., Hebbeln, D., Wienberg, C., 2008. Growth history of a cold-water coral covered carbonate mound - Galway Mound, Porcupine Seabight, NE-Atlantic. *Mar. Geol.* 253, 160–169.
- Erdey-Heydorn, M.D., 2008. An ArcGIS seabed characterization toolbox developed for investigating benthic habitats. *Mar. Geol.* 31, 318–358.
- Fink, H.G., Wienberg, C., De Pol-Holz, R., Wintersteller, P., Hebbeln, D., 2013. Cold-water coral growth in the Alboran Sea related to high productivity during the Late Pleistocene and Holocene. *Mar. Geol.* 339, 71–82.
- Flinch, J.F., Bally, A.W., Wu, S., 1996. Emplacement of a passive-margin evaporitic allochthon in the Betic Cordillera of Spain. *Geology* 24, 67–70.
- Foubert, A., Depreiter, D., Beck, T., Maignien, L., Panmémans, B., Frank, N., Blamart, D., Henriët, J.-P., 2008. Carbonate mounds in a mud volcano province off north-west Morocco: key to processes and controls. *Mar. Geol.* 248, 74–96.
- Frank, N., Freiwald, A., Lopez Correa, M., Wienberg, C., Eisele, M., Hebbeln, D., Van Rooij, D., Henriët, J.-P., Colin, C., van Weering, T., de Haas, H., Buhl-Mortensen, P., Roberts, J.M., De Mol, B., Douville, E., Blamart, D., Hatte, C., 2011. Northeastern Atlantic cold-water coral reefs and climate. *Geology* 39, 743–746.
- Frederiksen, R., Jensen, A., Westerberg, H., 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faeroe Islands and the relation to internal tidal mixing. *Sarsia* 77, 157–171.
- Glogowski, S., Dullo, W.C., Feldens, P., Liebetrau, V., von Reumont, J., Hühnerbach, V., Krastel, S., Wynn, R.B., Flögel, S., 2015. The Eugen Seibold coral mounds offshore western Morocco: oceanographic and bathymetric boundary conditions of a newly discovered cold-water coral province. *Geo-Mar. Lett.* 35, 257–269.
- Grant, K.M., Rohling, E.J., Ramsey, C.B., Cheng, H., Edwards, R.L., Florindo, F., Heslop, D., Marra, F., Roberts, A.P., Tamisieva, M.E., Williams, F., 2014. Sea-level variability over five glacial cycles. *Nat. Commun.* 5, 5076.
- Grasmueck, M., Eberli, G.P., Viggiano, D.A., Correa, T., Rathwell, G., Luo, J., 2006. Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the Straits of Florida. *Geophys. Res. Lett.* 33, L23616. <https://doi.org/10.1029/2006GL027734>.
- Greene, H.G., Yoklavich, M.M., Starr, R.M., O'Connell, V.M., Wakefield, W.W., Sullivan, D.E., McRea, J.E., Cailliet, G.M., 1999. A classification scheme for deep seafloor habitats. *Oceanol. Acta* 22, 663–678.
- Hamilton, E.L., 1976. Variations of density and porosity with depth in deep-sea sediments. *J. Sediment. Petrol.* 46, 280–300.
- Hebbeln, D., 2019. Highly variable submarine landscapes in the Alborán Sea created by cold-water corals. In: Orejas, C., Jiménez, C. (Eds.), *Mediterranean Cold-water Corals: Past, Present and Future*. Springer Series: Coral Reefs of the World (in press).
- Hebbeln, D., Samankassou, E., 2015. Where did ancient carbonate mounds grow — in bathyal depths or in shallow shelf waters? *Earth Sci. Rev.* 145, 56–65.
- Hebbeln, D., Wienberg, C., Cruise Participants, 2008. Report and preliminary results of RV Pelagia cruise 64PE284, Cold-water corals in the Gulf of Cádiz and on Coral Patch Seamount, Portimao - Portimao, 18.02.-09.03.2008. In: Reports of the Department of Geosciences. University of Bremen (GeoB), pp. 90 (No. 265).
- Hebbeln, D., Wienberg, C., Wintersteller, P., Freiwald, A., Becker, M., Beuck, L., Dullo, C., Eberli, G.P., Glogowski, S., Matos, L., Forster, N., Reyes-Bonilla, H., Taviani, M., 2014. Environmental forcing of the Campeche cold-water coral province, southern Gulf of Mexico. *Biogeosciences* 11, 1799–1815.
- Hebbeln, D., Wienberg, C., Cruise Participants, 2015. Report and Preliminary Results of R/V MARIA S. MERIAN Cruise MSM36. MoccoMeBo. Malaga - Las Palmas, February 18–March 17 2014. pp. 79. https://doi.org/10.2312/cr_msm36.
- Hebbeln, D., Van Rooij, D., Wienberg, C., 2016. Good neighbours shaped by vigorous currents: Cold-water coral mounds and contourites in the North Atlantic. *Mar. Geol.* 378, 171–185.
- Henriet, J.-P., De Mol, B., Pillen, S., Vanneste, M., Van Rooij, D., Versteeg, W., Croker, P.F., Shannon, P.M., Unnithan, V., Bouriak, S., Chachkine, P., 1998. Gas hydrate crystals may help build reefs. *Nature* 391, 647–649.
- Henriet, J.-P., Hamoumi, N., Da Silva, A.C., Foubert, A., Lauridsen, B.W., Rüggeberg, A., Van Rooij, D., 2014. Carbonate mounds: from paradox to World Heritage. *Mar. Geol.* 352, 89–110.
- Henry, L.-A., Roberts, J.M., 2017. Global biodiversity in cold-water coral reef ecosystems. In: Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C. (Eds.), *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. Springer, Cham, pp. 235–256.
- Hernández-Molina, F.J., Llave, E., Stow, D.A.V., 2008. Continental slope contourites. In: Rebesco, M., Camerlenghi, A. (Eds.), *Contourites: Developments in Sedimentology* 60. Elsevier, Amsterdam, pp. 379–407.
- Hernández-Molina, F.J., Llave, E., Preu, B., Ercilla, G., Fontan, A., Bruno, M., Serra, N., Gomez, J.J., Brackenridge, R.E., Sierro, F.J., Stow, D.A.V., García, M., Juan, C., Sandoval, N., Arnaiz, A., 2014. Contourite processes associated with the Mediterranean Outflow Water after its exit from the Strait of Gibraltar: Global and conceptual implications. *Geology* 42, 227–230.
- Huvenne, V.A.I., De Mol, B., Henriët, J.-P., 2003. A 3D seismic study of the morphology and spatial distribution of buried coral banks in the Porcupine Basin, SW of Ireland. *Mar. Geol.* 198, 5–25.
- Huvenne, V.A.I., Bailey, W.R., Shannon, P.M., Naeth, J., di Primio, R., Henriët, J.-P., Horsfield, B., de Haas, H., Wheeler, A.J., Olu-Le Roy, K., 2007. The Magellan mound province in the Porcupine Basin. *Int. J. Earth Sci.* 96, 85–101.
- Huvenne, V.A.I., Masson, D.G., Wheeler, A.J., 2009. Sediment dynamics of a sandy contourite: the sedimentary context of the Darwin cold-water coral mounds, Northern Rockall Trough. *Int. J. Earth Sci.* 98, 865–884.
- Le Guilloux, E., Olu-Le Roy, K., Bourillet, J.F., Savoye, B., Iglésias, S.P., Sibuet, M., 2009. First observations of deep-sea coral reefs along the Angola margin. *Deep-Sea Res. II* 56, 2394–2403.
- León, R., Somoza, L., Medialdea, T., Vázquez, J.T., González, F.J., López-González, N., Casas, D., del Pilar Mata, M., del Fernández-Puga, M.C., Giménez-Moreno, C.J., Díaz-del-Río, V., 2012. New discoveries of mud volcanoes on the Moroccan Atlantic continental margin (Gulf of Cádiz): morpho-structural characterization. *Geo-Mar. Lett.* 32, 473–488.
- Lindberg, B., Mienert, J., 2005. Postglacial carbonate production by cold-water corals on the Norwegian Shelf and their role in the global carbonate budget. *Geology* 33, 537–540.
- Lo Iacono, C., Gràcia, E., Ranero, C.R., Emelianov, M., Huvenne, V.A.I., Bartolomé, R., Booth-Rea, G., Prades, J., 2014. The West Melilla cold water coral mounds, Eastern Alboran Sea: morphological characterization and environmental context. *Deep-Sea Res. II* 99, 316–326.
- Louarn, E., Morin, P., 2011. Antarctic intermediate water influence on Mediterranean sea water outflow. *Deep-Sea Res. II* 58, 932–942.
- Lüdmann, T., Paulat, M., Möbius, J., Lindhorst, S., Wunsch, M., Eberli, G.P., 2016. Carbonate mounds in the Santaren Channel, Bahamas: a current-dominated periplatform depositional regime. *Mar. Geol.* 376, 69–85.
- Machín, F., Pelegrí, J.L., Marrero-Díaz, A., Laiz, I., Ratsimandresy, A.W., 2006. Near-surface circulation in the southern Gulf of Cádiz. *Deep-Sea Res. II* 53, 1161–1181.
- Maldonado, A., Somoza, L., Pallares, L., 1999. The Betic orogen and the Iberian-African boundary in the Gulf of Cádiz: geological evolution (central North Atlantic). *Mar. Geol.* 155, 9–43.
- Masson, D., Bett, B., Billett, D.S., Jacobs, C., Wheeler, A., Wynn, R., 2003. The origin of deep-water, coral-topped mounds in the northern Rockall Trough, Northeast Atlantic. *Mar. Geol.* 194, 159–180.
- Matos, L., Wienberg, C., Titschack, J., Schmied, G., Frank, N., Abrantes, F., Cunha, M.R., Hebbeln, D., 2017. Coral mound development at the Campeche cold-water coral province, southern Gulf of Mexico: implications of Antarctic Intermediate Water increased influence during interglacials. *Mar. Geol.* 392, 53–65.
- Medialdea, T., Vegas, R., Somoza, L., Vázquez, J.T., Maldonado, A., Díaz del Río, V., Maestro, A., Córdoba, D., Fernández-Puga, M.C., 2004. Structure and evolution of the “Oligostrome” complex of the Gibraltar Arc in the Gulf of Cádiz (eastern Central Atlantic): evidence from two long seismic cross-sections. *Mar. Geol.* 209, 173–198.
- Messing, C.G., Neumann, A.C., Lang, J.C., 1990. Biozonation of deep-water lithoherms and associated hardgrounds in the northeastern Straits of Florida. *Palaios* 5, 15–33.
- Mienis, F., de Stigter, H.C., White, M., Duineveld, G., de Haas, H., van Weering, T.C.E., 2007. Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough margin, NE Atlantic Ocean. *Deep-Sea Res.* 1 54, 1655–1674.
- Mienis, F., De Stigter, H.C., De Haas, H., Van der Land, C., Van Weering, T.C.E., 2012. Hydrodynamic conditions in a cold-water coral mound area on the Renard Ridge, southern Gulf of Cádiz. *J. Mar. Syst.* 96–97, 61–71.
- Mienis, F., Duineveld, G.C.A., Davies, A.J., Lavaleye, M.M.S., Ross, S.W., Seim, H., Bane, J., van Haren, H., Bergman, M.J.N., de Haas, H., Brooke, S., van Weering, T.C.E., 2014. Cold-water coral growth under extreme environmental conditions, the Cape Lookout area, NW Atlantic. *Biogeosciences* 11, 2543–2560.
- Millman, J.D., 1993. Production and accumulation of calcium carbonate in the ocean: budget of a nonsteady state. *Glob. Biogeochem. Cycles* 7, 927–957.
- Mortensen, P.B., Hovland, M., Fosså, J.H., Furevik, D.M., 2001. Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. *J. Mar. Biol. Assoc. U. K.* 51, 999–1013.

- Muñoz, A., Cristobo, J., Rios, P., Druet, M., Polonio, V., Uchupi, E., Acosta, J., 2012. Sediment drifts and cold-water coral reefs in the Patagonian upper and middle continental slope. *Mar. Pet. Geol.* 36, 70–82.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S., McGuire, A.D., Piao, S., Rautiainen, A.M., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 1201609.
- Pfannkuche, O., Shipboard Scientific Party, 2007. Cruise Report Maria S. Merian 1/3, 12.04.-19.05.2006. IFM-GEOMAR, Kiel, Germany, pp. 115.
- Pinheiro, L.M., Ivanov, M.K., Sautkin, A., Akhmanov, G., Magalhaes, V.H., Volkonskaya, A., Monteiro, J.H., Somoza, L., Gardner, J., Hamouni, N., Cunha, M.R., 2003. Mud volcanism in the Gulf of Cádiz: results from the TTR-10 cruise. *Mar. Geol.* 195, 131–151.
- Pomar, L., Morsilli, M., Hallock, P., Bádenas, B., 2012. Internal waves, an under-explored source of turbulence events in the sedimentary record. *Earth Sci. Rev.* 111, 56–81.
- Raddatz, J., Rüggeberg, A., Liebetrau, V., Foubert, A., Hathorne, E.C., Fietzke, J., Eisenhauer, A., Dullo, W.-C., 2014. Environmental boundary conditions of cold-water coral mound growth over the last 3 million years in the Porcupine Seabight, Northeast Atlantic. *Deep-Sea Res. II* 99, 227–236.
- Ramos, A., Sanz, J.L., Ramil, F., Agudo, L.M., Presas-Navarro, C., 2017. The giant cold-water coral mounds barrier off Mauritania. In: Ramos, A., Ramil, F., Sanz, J.L. (Eds.), *Deep-sea Ecosystems off Mauritania: Research of Marine Biodiversity and Habitats in the Northwest African Margin*. Springer Netherlands, Dordrecht, pp. 481–525.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., Cairns, S.D., 2009. *Cold-water Corals. The Biology and Geology of Deep-sea Coral Habitats*. Cambridge University Press, Cambridge, UK.
- Rüggeberg, A., Dullo, W.-C., Dorschel, B., Hebbeln, D., 2007. Environmental changes and growth history of a cold-water carbonate mound (Propeller Mound, Porcupine Seabight). *Int. J. Earth Sci.* 96, 57–72.
- Savini, A., Corselli, C., 2010. High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca Cold Water Coral province (Northern Ionian Sea—Apulian continental slope). *Deep-Sea Res. II* 57, 326–344.
- Smith, S.V., Mackenzie, F.T., 2016. The role of CaCO₃ reactions in the contemporary oceanic CO₂ cycle. *Aquat. Geochem.* 22, 153–175.
- Somoza, L., Diaz-del-Rio, V., Leon, R., Ivanov, M., Fernandez-Puga, M.C., Gardner, J.M., Hernandez-Molina, F.J., Pinheiro, L.M., Rodero, J., Lobato, A., 2003. Seabed morphology and hydrocarbon seepage in the Gulf of Cádiz mud volcano area: acoustic imagery, multibeam and ultra-high resolution seismic data. *Mar. Geol.* 195, 153–176.
- Thierens, M., Titschack, J., Dorschel, B., Huvenne, V.A.I., Wheeler, A.J., Stuut, J.B., O'Donnell, R., 2010. The 2.6 Ma depositional sequence from the Challenger cold-water coral carbonate mound (IODP Exp. 307): Sediment contributors and hydrodynamic palaeo-environments. *Mar. Geol.* 271, 260–277.
- Thierens, M., Browning, E., Pirlet, H., Loutre, M.F., Dorschel, B., Huvenne, V.A.I., Titschack, J., Colin, C., Foubert, A., Wheeler, A.J., 2013. Cold-water coral carbonate mounds as unique palaeo-archives: the Plio-Pleistocene Challenger Mound record (NE Atlantic). *Quat. Sci. Rev.* 73, 14–30.
- Titschack, J., Thierens, M., Dorschel, B., Schulbert, C., Freiwald, A., Kano, A., Takashima, C., Kawagoe, N., Li, X., 2009. Carbonate budget of a cold-water coral mound (Challenger Mound, IODP Exp. 307). *Mar. Geol.* 259, 36–46.
- Titschack, J., Baum, D., De Pol Holz, R., López Correa, M., Forster, N., Flögel, S., Hebbeln, D., Freiwald, A., 2015. Aggradation and carbonate accumulation of Holocene Norwegian cold-water coral reefs. *Sedimentology* 62, 1873–1898.
- Titschack, J., Fink, H.G., Baum, D., Wienberg, C., Hebbeln, D., Freiwald, A., 2016. Mediterranean cold-water corals – an important regional carbonate factory? *Depos. Rec.* 2, 74–96.
- Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A., 2002. Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. *The Holocene* 12, 69–80.
- Van Rensbergen, P., Depreiter, D., Pannemans, B., Moerkerke, G., Van Rooij, D., Marsset, B., Akhmanov, G., Blinova, V., Ivanov, M., Rachidi, M., 2005. The El Arraiche mud volcano field at the Moroccan Atlantic slope, Gulf of Cádiz. *Mar. Geol.* 219, 1–17.
- Van Rooij, D., Huvenne, V., Moerkerke, G., Henriët, J.-P., 2002. Cruise Report, RV Belgica Cruise 02/12, CADIPOR I (Gulf of Cádiz), Brest - Lissabon - Cádiz, 11.05.-28.05.2002. Renard Centre of Marine Geology (RCMG), University of Ghent, Belgium, pp. 30.
- Van Rooij, D., Depreiter, D., Bouimetarhan, I., De Boever, E., De Rycker, K., Foubert, A., Huvenne, V., Réveillaud, J., Staelens, P., Vercruysee, J., Versteeg, W., Henriët, J.-P., 2005. First sighting of active fluid venting in the Gulf of Cádiz. *Eos* 86, 509–511.
- Van Rooij, D., Blamart, D., De Mol, L., Mienis, F., Pirlet, H., Wehrmann, L.M., Barbieri, R., Maignien, L., Templer, S.P., de Haas, H., Hebbeln, D., Frank, N., Larmagnat, S., Stadrnitskaia, A., Stivaletta, N., van Weering, T., Zhang, Y., Hamoumi, N., Cnudde, V., Duyck, P., Henriët, J.P., 2011. Cold-water coral mounds on the Pen Duick Escarpment, Gulf of Cádiz: the MiCROSYSTEMS project approach. *Mar. Geol.* 282, 102–117.
- Van Rooij, D., Hebbeln, D., Comas, M., Vandorpe, T., Delivet, S., Nave, S., Michel, E., Lebreiro, S., Terrinha, P., Roque, C., 2013. MD 194/EUROFLEETS à bord du R/V Marion Dufresne. Cadix 10 juin 2013-Lisbonne 20 juin 2013.
- Vandorpe, T., Van Rooij, D., de Haas, H., 2014. Stratigraphy and paleoceanography of a topography-controlled contourite drift in the Pen Duick area, southern Gulf of Cádiz. *Mar. Geol.* 349, 136–151.
- Vandorpe, T., Martins, I., Vitorino, J., Hebbeln, D., García, M., Van Rooij, D., 2016. Bottom currents and their influence on the sedimentation pattern in the El Arraiche mud volcano province, southern Gulf of Cádiz. *Mar. Geol.* 378, 114–126.
- Vandorpe, T., Wienberg, C., Hebbeln, D., Van den Berghe, M., Gaide, S., Wintersteller, P., Van Rooij, D., 2017. Multiple generations of buried cold-water coral mounds since the Early-Middle Pleistocene transition in the Atlantic Moroccan Coral Province, southern Gulf of Cádiz. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 485, 293–304.
- Viana, A.R., Faugeres, J.C., Kowmann, R.O., Lima, J.A.M., Caddah, L.F.G., Rizzo, J.G., 1998. Hydrology, morphology and sedimentology of the Campos continental margin, offshore Brazil. *Sediment. Geol.* 115, 133–157.
- Victorero, L., Blamart, D., Pons-Branchu, E., Mavrogordato, M.N., Huvenne, V.A.I., 2016. Reconstruction of the formation history of the Darwin Mounds, N Rockall Trough: how the dynamics of a sandy contourite affected cold-water coral growth. *Mar. Geol.* 378, 186–195.
- Weiss, A., 2001. Topographic position and landforms analysis. In: Poster Presentation, ESRI User Conference, San Diego, CA.
- Wessel, P., Smith, W.H.F., 1998. New, improved version of generic mapping tools released. *Eos* 79, 579.
- Wheeler, A.J., Beyer, A., Freiwald, A., de Haas, H., Huvenne, V.A.I., Kozachenko, M., Olu-Le Roy, K., Operbecke, J., 2007. Morphology and environment of cold-water coral carbonate mounds on the NW European margin. *Int. J. Earth Sci.* 96, 37–56.
- White, M., Dorschel, B., 2010. The importance of the permanent thermocline to the cold water coral carbonate mound distribution in the NE Atlantic. *Earth Planet. Sci. Lett.* 296, 395–402.
- White, M., Mohn, C., de Stigter, H., Mottram, G., 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer, Heidelberg, pp. 503–514.
- Wienberg, C., Titschack, J., 2017. Framework-forming scleractinian cold-water corals through space and time: a late Quaternary North Atlantic perspective. In: Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C. (Eds.), *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. Springer, Cham, pp. 699–732.
- Wienberg, C., Hebbeln, D., Fink, H.G., Mienis, F., Dorschel, B., Vertino, A., Lopez Correa, M., Freiwald, A., 2009. Scleractinian cold-water corals in the Gulf of Cádiz - first clues about their spatial and temporal distribution. *Deep-Sea Res. I* 56, 1873–1893.
- Wienberg, C., Frank, N., Mertens, K.N., Stuut, J.-B., Marchant, M., Fietzke, J., Mienis, F., Hebbeln, D., 2010. Glacial cold-water coral growth in the Gulf of Cádiz: Implications of increased palaeo-productivity. *Earth Planet. Sci. Lett.* 298, 405–416.
- Wienberg, C., Titschack, J., Freiwald, A., Frank, N., Lundlöv, T., Taviani, M., Beuck, L., Schröder-Ritzrau, A., Kregel, T., Hebbeln, D., 2018. The giant Mauritanian cold-water coral mound province: oxygen control on coral mound formation. *Quat. Sci. Rev.* 185, 135–152.
- Wright, D.J., Lundblad, E.R., Larkin, E.M., Rinehart, R.W., Murphy, J., Cary-Kothera, L., Draganov, K., 2005. ArcGIS Benthic Terrain Modeler. Oregon State University, Davey Jones Locker Seafloor Mapping/Marine GIS Laboratory and NOAA Coastal Services Center, Corvallis, Oregon Accessible online at: <http://www.csc.noaa.gov/products/btm/>.
- Zitellini, N., Gràcia, E., Matias, L., Terrinha, P., Abreu, M.A., DeAlteriis, G., Henriët, J.P., Dañobeitia, J.J., Masson, D.G., Mulder, T., Ramella, R., Somoza, L., Diez, S., 2009. The quest for the Africa-Eurasia plate boundary west of the Strait of Gibraltar. *Earth Planet. Sci. Lett.* 280, 13–50.