

Environmental forcing of the Campeche cold-water coral province

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Environmental forcing of the Campeche cold-water coral province, southern Gulf of Mexico

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With an extension of $> 40 \text{ km}^2$ the recently discovered Campeche cold-water coral province located at the northeastern rim of the Campeche Bank in the southern Gulf of Mexico belongs to the largest coherent cold-water coral areas discovered so far. The Campeche province consists of numerous 20 to 40 m high coral ridges that are developed in intermediate water depths of 500 to 600 m. The ridges are colonized by a vivid cold-water coral ecosystem that covers the upper flanks and summits. The rich coral community is dominated by the framework-building scleractinia *Enallopsammia profunda* and *Lophelia pertusa* while the associated benthic megafauna shows a rather scarce occurrence. The recent environmental setting is characterized by a high surface water production caused by a local upwelling center and a dynamic bottom water regime comprising vigorous bottom currents, internal waves and strong density contrasts, which all together provide optimal conditions for the growth of cold-water corals. The strong hydrodynamics – potentially supported by the diel vertical migration of zooplankton in the Campeche area – drive the delivering of food particles to the corals. The Campeche cold-water coral province is, thus, an excellent example highlighting the importance of the hydrographic setting in securing the food supply for the development of large and vivid cold-water coral ecosystems.

1 Introduction

The last decade has witnessed a tremendous progress in our knowledge about “framework-building cold-water corals” (CWC) as their role as ecosystem engineers creating highly diverse ecosystems in water depths far beyond the shelf edge is becoming more and more obvious (Roberts et al., 2009). The biodiversity associated with these ecosystems may be comparable to that found in tropical coral reefs (Roberts et al., 2006), and they occur almost world-wide except only for the highest latitudes (Davies and Guinotte, 2011). The availability of advanced deep-sea technologies (e.g.,

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remotely operated vehicles) greatly supported the discovery and investigation of large, thriving and (so far) unknown CWC ecosystems in remote places. Successful studies such as those performed off Mauritania (Colman et al., 2005), off Angola (Le Guilloux et al., 2009), and in various parts of the Mediterranean Sea (Freiwald et al., 2009; Orejas et al., 2009; Fink et al., 2013; Gori et al., 2013), demonstrate the potential use of these technologies for future discoveries.

With their rigid carbonate skeletons that can persist over geological time scales the CWC shape the sea floor by creating large three-dimensional structures, e.g., > 300 m-high coral carbonate mounds along the Irish margin (e.g., Kenyon et al., 2003; Mienis et al., 2007) reaching back to Pliocene times (~ 2.6 Ma; Kano et al., 2007) and > 100 km²-large reef/ridge structures off Norway (Fosså et al., 2005) formed during the Holocene (e.g., López Correa et al., 2012). These structures consist of a mixture of coral skeletons, the skeletal remains of the coral-associated megafaunal community, and pelagic or hemipelagic sediments that can serve as paleo-environmental archives allowing to reconstruct the long-term development of the CWC ecosystems (e.g., Dorschel et al., 2005; Frank et al., 2009; Titschack et al., 2009; Wienberg et al., 2009; Eisele et al., 2011; Fink et al., 2012; López Correa et al., 2012; Douarin et al., 2013; Thierens et al., 2013).

The scleractinian *Lophelia pertusa* is among the most common and most widespread CWC species world-wide and is particularly abundant in the NE Atlantic (Davies and Guinotte, 2011). This species withstands a rather wide range of physico-chemical conditions (see summary in Davies et al., 2008), a fact that explains its almost global distribution in depths between a few tens of meters and over 2000 m (Freiwald and Roberts, 2005). Another critical factor controlling its distribution is sufficient food supply that is commonly driven by the interplay of surface water productivity and the strength of the bottom current regime (e.g., currents, internal waves and tides) delivering food particles to the CWC (Duineveld et al., 2004, 2007; White et al., 2005). Paleo-environmental studies revealed that food supply often is the decisive factor triggering on- or off-sets

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of coral growth in a given setting (e.g., Dorschel et al., 2005; Wienberg et al., 2010; Eisele et al., 2011; Fink et al., 2013).

In addition to the CWC hotspot in the NE Atlantic, *L. pertusa* also contributes to numerous coral mound and ridge structures in the NW Atlantic along the continental margin from North Carolina (Ross and Nizinski, 2007), along the Florida-Hatteras slope (Paull et al., 2010), and the Bahamas to the Florida Straits (e.g., Neumann et al., 1977; Mullins et al., 1981; Grasmueck et al., 2006; Correa et al., 2012a, 2012b). Further west in the Gulf of Mexico, *L. pertusa* appears to be more scattered, forming isolated mound-like structures along the West Florida slope (Newton et al., 1987; Hübscher et al., 2010) and in the northern Gulf of Mexico (Moore and Bullis, 1960; Schroeder, 2002; Reed et al., 2006; Cordes et al., 2008; Becker et al., 2009; Davies et al., 2010). Summarizing the current knowledge, Mienis et al. (2012) conclude that within the Gulf of Mexico CWC mound structures have been rarely found, except on the West Florida slope and in the Viosca Knoll area (Fig. 1). The latter area has been considered the most extensive *Lophelia* habitat found so far in this region (Brooke and Schroeder, 2007; Davies et al., 2010) probably as a consequence of enhanced productivity driven by nutrient-enriched Mississippi River outflow (Wawrik and Paul, 2004). Apart from the Campeche Bank, the southern Gulf of Mexico is generally characterized by meager planktonic biomass along the Mexican slope mirroring the low-productivity Caribbean water that enters the Gulf of Mexico through Yucatan Strait (Wei et al., 2012).

In this paper, we document for the first time build-ups at the sea floor formed by framework-building scleractinian corals on the slope of the Mexican Campeche Bank, southern Gulf of Mexico. These build-ups are mainly formed by an *Enallopsammia profunda* – *Lophelia pertusa* community. This finding was unexpected as available data from a few dredge haul stations only described the occurrence of the scleractinian CWC *Madrepora oculata* along the margin of the Campeche Bank, north of the Mexican Yucatan peninsula (Cairns, 1979; Schroeder et al., 2005). Only in 2010 more detailed information was provided, when hydroacoustic surveys revealed “mound-like” structures between 500 and 600 m water depth along the margin of the bank (Hübscher

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sites near the Campeche CWC province can appear prominently in satellite-based productivity maps (Fig. 1).

Along its eastern edge the Campeche Bank borders the Yucatan Strait that forms the main passage connecting the Caribbean Sea and the Gulf of Mexico through which the Yucatan Current transports ~ 24 Sv from South to North (Sheinbaum et al., 2002). According to Merino (1997) three main water masses comprise the water column there. Salinity and temperature increase together from the Antarctic Intermediate Water (AAIW, 7°C , salinity 34.9) in the deep towards the salinity maximum of the Subtropical Intermediate Water (STUW, 23°C , salinity 36.8) at ~ 150 m depth. Further above temperature rises and salinity declines until from 50 m to the surface both parameters remain relatively constant (26 – 27.5°C , salinity < 36.4) representing the Caribbean Surface Water (CSW). In depths greater than ~ 650 m, the Yucatan Countercurrent transports water southward while being confined to the western, Mexican side of the Yucatan Strait (Sheinbaum et al., 2002).

With respect to the strength of the bottom current regime, the best information is provided by mooring data obtained slightly further south in the Yucatan Strait ($\sim 21.5^\circ\text{N}$; e.g., Sheinbaum et al., 2002). Along a W–E transect through the area, the mean northward current velocities at the western margin decrease rapidly from almost 100 cm s^{-1} at the surface to $< 10\text{ cm s}^{-1}$ in 200 m water depth. However, at the depth of the Campeche CWC province (~ 550 m at 23.8°N) the bottom current velocities in the Yucatan Strait (21.5°S) increase again to $> 10\text{ cm s}^{-1}$.

3 Methods

All data presented here were collected during expedition MSM 20-4 with the German R/V *Maria S. Merian* in spring 2012 (Hebbeln et al., 2012). They include hydroacoustic measurements, water column studies, and seabed ROV video observation and sampling (see Table 1 and Fig. 2 for relevant site information). Instrument specifications and applied settings for the hydroacoustic measurements are described in detail in

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Hebbeln et al. (2012). For all hydroacoustic measurements introduced below, the essential sound velocity profile through the water column has been obtained from two CTD casts in (GeoB 16305-1) and close (GeoB 16303-1) to the working area (Figs. 1 and 2, Table 1).

3.1 Hydroacoustic measurements

3.1.1 Multibeam echosounder (MBES)

Seabed mapping was performed using a KONGSBERG EM1002 multibeam echosounder system (MBES), which operates at a frequency of 95 kHz. The EM1002 uses 111 beams per ping, covers a depth range of 2 to 1000 m and achieves a high depth resolution of 2–8 cm, depending on the pulse length (0.2–2 ms). Achievable swath width on a flat bottom is up to 5 times the water depth dependent on the character of the seafloor. Spatial integrity of the mapping data was achieved by combining the ship's SEAPATH 200 Inertial Navigation System (INS) including Differential Global Positioning System (DGPS) information with motion 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 evaluation. ESRI ArcGIS v.10 was used to create maps (grid cell size: 10 m) and a sustainable spatial data management.

3.1.2 Acoustic Doppler Current Profiler (ADCP)

Current velocity and direction, and backscatter data through the water column were measured with an RDI Ocean Surveyor Acoustic Doppler Current Profiler (ADCP), which operates at a frequency of 75 kHz. Data were acquired using the RDI software VMDAS (Vessel-Mount Data Acquisition) using 128 depth bins of 5 m bin size. Backscatter data were corrected for beam spreading and water absorption (Deines,

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them (Fig. 3). However, on some steeply inclined ridges (up to 30°), coral colonization starts already at the base of the current-exposed side of the ridges, thereby generating a sharp change of sedimentary facies from pelagic muds to a living CWC ecosystem. On less steep ridges live coral colonies start to appear halfway upslope the current-exposed flank, or the ridge flanks are entirely covered by a dead and collapsed coral framework or coral rubble with only few live coral colonies in between. For both types of ridges, corals fade off halfway along the leeward flanks of the ridges. Overall, the density of coral framework and the proportion of live coral colonies become progressively higher towards the summit, thus forming very dense coral thickets up to 60 cm thick in the summit area. The ridge flanks are dominated by *E. profunda* whereas *L. pertusa* becomes increasingly abundant, if not dominant on the summits.

The dendroid *E. profunda* colonies display an open-spaced growth habit with individual colony branches pointing to all directions (Fig. 4). This growth habit results in a loose mesh of coral framework thus facilitating framework disintegration of individual branches into stick-like fragments. Colony heights vary from 20 to 60 cm, thereby only the upper 10–15 cm of a colony yields live coral polyps and translucent tissue. *Lophelia pertusa* also constructs an open-spaced coral framework. However, secondary fusion between adjacent coral branches is a very common feature, thus increasing the structural integrity of the entire framework considerably in comparison to *E. profunda*. The branches of *L. pertusa* are strongly calcified and slender with individual corallite lengths of 2.5–3.5 cm and calicular diameters of 0.5–0.8 cm. This phenotype has been described as forma *gracilis* by Duncan (1873) and is in contrast to the stout branches with extremely wide calicular diameters of the *brachycephala* form (Fig. 4) described by Moseley (1881) and Cairns (1979). The latter phenotype occurs in low numbers in the Campeche CWC province but the co-occurrence of the two *L. pertusa* growth forms is a well-known phenomenon in the northern Gulf of Mexico (Newton et al., 1987; Brooke et al., 2009). The *Lophelia* framework can attain heights of 50 cm and the zone of live polyps and translucent tissue coverage stretch over a range of 20–30 cm.

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The live coral zone is utilized by the associated community in various ways and differs largely in terms of species composition and richness from the associated community found in the tissue-barren, exposed coral framework beneath. Common organisms observed (although not exclusively) in the live zone are the predatory decapods *Bathynectes longispina*, *Eumunida picta*, *Chaceon fenneri*, *Munidopsis* sp. and *Rochinia crassa* and the grazing echinoids *Cidaris* sp. and *Gracilechinus* sp. (Fig. 4). The latter echinoid has been recognized as a corallivore in CWC habitats of the eastern North Atlantic (Stevenson and Rocha, 2013). Other organisms with corallivore affinities in the live coral zone are hippasterinid star fishes (Mah et al., 2010) and the muricid gastropod *Coralliophila richardi* (Taviani et al., 2009), which we commonly collected from the live coral zone. Stalkless crinoids occasionally take advantage of the elevated and current-exposed position of live coral branches for filtering particles from the water. Indication of probably necrotic epibiosis of live scleractinians by zoanthids and actinarians in some scleractinian colonies is a common feature and seems to cause local mortality. Polychaetes of the Genus *Eunice*, from which several species are known as symbionts of *L. pertusa* and other colonial CWC (e.g., Buhl-Mortensen and Mortensen, 2004; Mueller et al., 2013) are surprisingly rare in the Campeche CWC province.

Characteristic organisms of the tissue-barren, exposed coral framework are fly-trap anemones (probably *Actinoscyphia* sp.; Fig. 4), isidid corals (*Keratoisis* sp.), and solitary scleractinians (*Desmophyllum dianthus*, *Javania cailetti*, *Stenocyathus vermiformis*, *Trochopsammia infundibulum*). The glass sponge *Aphrocallistes* sp. was found attached to the coral framework. Apparently the glass sponges are living together with masses of yellow actinarians (Fig. 4), thus resembling the recently described symbiotic relationship between the glass sponge *Hyalonema sieboldi* with the actinarian *Spongiactis japonica* (Sanamyan et al., 2012). Common fishes encountered frequently in the coral framework were *Helicolenus dactylopterus* and *Nettenchelys exoria*. The elsewhere common gorgonians and antipatharians are extremely rare.

The coral rubble is strongly admixed with unconsolidated pelagic mud thereby providing small hard-substrate islands within soft sediment. Common megafaunal organisms

are large astrorhizid foraminifers, cerianthids, pennatulaceans, stalked glass sponges (*Hyalonema* sp.), and the common decapods (same as in the live zone) and shrimps. Amongst the mobile organisms, the giant isopod crustacean *Bathynomus giganteus* was detected (Fig. 4). Like in other coral rubble habitats elsewhere in the Gulf of Mexico and in the northern Atlantic, the anglerfish *Chaunax suttkusi* (Fig. 4), was commonly spotted near the coral ridges resting on the seabed (Caruso et al., 2007). Other common fishes observed in the coral rubble and pelagic mud areas are *Chlorophthalmus agassizi*, *Laemonema* sp., *Nezumia* sp., Phycidae and Rajidae.

4.3 Water column structure/dynamics

The CTD measurements allow the identification of the most important regional water masses, based on temperature (potential temperature) and mainly on salinity data (Fig. 5). The uppermost ~ 80 m of the water column are characterized by the occurrence of water with salinities of < 36.4 indicative for the presence of the CSW. The salinity maximum (~ 36.8) between 100 and 160 m water depth is characteristic for the STUW. In 540 m water depth salinity drops below 35.0 marking the presence of (at least some) AAIW. In the depth range where living CWC have been observed during video observation (520 to 580 m) temperatures range between 9.5 and 7.5 °C and salinities between 35.1 and 34.9. Dissolved oxygen contents vary between 2.8 and 2.74 mL L⁻¹.

The Yoyo-CTD station (GeoB 16316) consisting of 13 individual, hourly taken casts reveal small, but significant variations in the deepest part of the water column just above the Campeche CWC province. For example, at 519 m water depth the temperature varies by almost 1 °C in approximately three cycles, each lasting three to six hours (Fig. 6a). These temperature changes are also reflected in the depth position of individual isotherms (8 to 9.5 °C, Fig. 6b). They fluctuate vertically by up to 20 m forced by the same cyclicity, and thus, most likely reflect the presence of internal waves. Along with these waves a distinct density gradient induced by temperature and salinity changes, almost reaching 0.7 °C and 0.07, respectively, over a 10 m depth interval (Fig. 6c) propagates across the site. With ~ 0.06 kg m⁻³ per 10 m depth interval this density gradient

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is strongest at 525 m depth and significantly higher than the average density gradient of 0.014 kg m^{-3} per 10 m depth interval that is observed for the entire lower water column between 250 m water depth and the seafloor.

The ADCP data collected over a 13 h time interval (simultaneously to the Yoyo-CTD data; see Table 1) allow to distinguish between three major layers that show some internal (although less pronounced) horizontal structuring (Fig. 7). Within the upper 130 m of the water column, the highest current velocities ($74\text{--}83 \text{ cm s}^{-1}$) occur together with a high backscatter ($94\text{--}98 \text{ dB}$). Current directions vary between 322° and 335° . The second layer between 130 and 460 m is characterized by continuously decreasing current velocities from 63 to 42 cm s^{-1} , again by rather stable current directions similar to the uppermost layer (325° to 336°), and by low backscatter values ($84\text{--}94 \text{ dB}$). The bottom layer ($> 460 \text{ m}$) is marked by a significant change in current direction (343° to 360°) and by the lowest but still strong currents flowing with 24 to 42 cm s^{-1} .

At the beginning of the stationary ADCP record (ca. 00:00 UTC, 24 March 2012) enhanced backscatter signals move upward through the water column towards the sea surface. By the end (ca. 11:30 UTC), similar signals move downward towards the seabed (Fig. 7). Similar observations were made during additional ADCP surveys in the working area during cruise MSM20-4 (Hebbeln et al., unpubl. data). In total, four upward (always at around 0:00 UTC, corresponding to 18:15 h local “solar” time at 86° W , i.e. sunset) and two downward movements (always at around 11:30 UTC, corresponding to 5:45 h local “solar” time at 86° W , i.e. sunrise) were observed.

5 Discussion

Large CWC-formed seafloor structures have been reported from many regions in the world’s oceans (see compilation in Freiwald and Roberts, 2005). In addition to the $> 300 \text{ m}$ high CWC mounds off Ireland (Kenyon et al., 2003; Mienis et al., 2007; Dorschel et al., 2010), the extensive reefs off Norway (e.g., Fosså et al., 2005) are the most impressive features. Extending over tens of kilometers (e.g., the Sula Reef,

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~ 14 km × 0.5 km, Freiwald et al., 2002; the Røst Reef, ~ 40 km × 3 km, Fosså et al., 2005) and reaching up to ~ 40 m in height these reefs generally comprise clusters of individual frameworks rather than a single coalescent structure (Freiwald et al., 2002). The Campeche CWC province shows a similar appearance as it comprises a cluster of individual coral ridges rather than a single clearly confined reef structure. The term “province” is used for the present study to describe the CWC ridges along the Campeche Bank following the nomenclature developed for the Irish margin where numerous individual CWC mounds and ridges occur clustered in provinces (e.g., White and Dorschel, 2010). With its mapped area of 10 km × 4 km, and most likely further northwest- and southeastward extensions, the Campeche CWC province reaches up with the large Norwegian reefs and, thus, belongs to the largest mapped CWC structures in the world. In addition, the Campeche CWC province represents the most important and extensive flourishing azooxanthellate coral area in the entire Gulf of Mexico discovered so far. The geographically closest CWC province is situated along the Miami Terrace in the Straits of Florida, where 27 km² of coral ridges are mapped in detail by an autonomous under water vehicle (Correa et al., 2012a) in an area where earlier studies have reported occurrences of “muddy mounds” and “sand ridges” (Neumann and Ball, 1970).

Whereas the large Irish coral mounds have been accumulated over > 2 million years (Kano et al., 2007), the Norwegian reefs have been formed only during the last ~ 10 000 yr of the Holocene (e.g., López Correa et al., 2012), when during the last deglaciation the Fennoscandian Ice Sheet retreated beyond the present-day coastline. However, the size of such structures cannot easily be transferred into age, as, for example, the Irish mounds at some point in time changed from a distinct accumulation stage into an almost stagnation stage marked by CWC growth and sediment deposition alternating with extensive periods dominated by erosion (Dorschel et al., 2005; Kano et al., 2007; Eisele et al., 2008). Thus, the average height of the Campeche coral ridges of 20 to 40 m does not allow for estimating the onset of coral growth in the region. Nevertheless, their size and the collection of a > 10 m long sediment core

containing abundant coral fragments embedded in a matrix of hemipelagic sediments (Hebbeln et al., 2012) reveal that also this CWC ecosystem has a relevant, although yet not constrained history.

A PARASOUND sediment echosounder profile crossing the Campeche CWC province from west to east displays a strong reflection underneath the drift sediment bodies and the CWC ridges developed along the Campeche Bank slope (Hübscher et al., 2010). It is assumed that this continuous strong reflector forms the base of the coral ridges (Hübscher et al., 2010) that might have provided the hardground allowing for the initial coral settlement similar to the erosional unconformity forming the base of the Irish CWC mounds (Van Rooij et al., 2003; Kano et al., 2007). The coral ridges show little to no internal layering and are often transparent. The lack of a strong top reflection indicates little or no cementation of the coral ridges.

CWC are often forming coral mounds that can have a variety of shapes from circular to elongate (Roberts et al., 2009). Elongated mounds turning into ridges often have been related to bottom current activity, however, with coral ridges sometimes occurring perpendicular (Correa et al., 2012a) and sometimes parallel (Messing et al., 1990) to the main current direction. The coral ridges within the Campeche CWC province appear to be generally aligned parallel to the main current direction possibly following an upstream growth pattern as outlined by Messing et al. (1990). They mostly stretch towards 330° with some heading towards 300° . These directions are close to the two main current directions of 330° (above ~ 470 m) and 360° (below ~ 470 m) derived from the ADCP data (Fig. 7) which, however, only represent a snapshot in time. Temporal variations (e.g., lunar, seasonal) in the depth layer of the change in current direction might result in the different directions of the coral ridges observed. Then, the 30° offset between both current directions and both ridge configurations observed could speculatively related to an inherent 30° relationship between coral ridge growth and prevailing current direction. However, also temporal changes in the actual current direction, not covered during this short survey, may account for this offset.

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5.1 The Campeche cold-water corals and associated community

The Campeche CWC province is constructed by *Enallopsammia profunda* and to a lesser degree by *Lophelia pertusa*. Neither of the scleractinians have been reported in previous publications from the Campeche slope (e.g., Cairns, 1979; Cairns et al., 1993) but are known from several locations in the Caribbean Sea and northern Gulf of Mexico (see compilations of published and unpublished information by Brooke and Schroeder, 2007; Lutz and Ginsburg, 2007; Messing et al., 2008). While *L. pertusa* has a nearly cosmopolitan distribution, *E. profunda* is endemic to the western Atlantic from the Antilles in the south to off Massachusetts in the north at water depths of 146–1748 m (Cairns, 1979). Structure-forming *Enallopsammia-Lophelia* frameworks are known from the base of the Florida-Hatteras slope in 500–800 m water depth and from Miami to South Carolina (Reed, 2002). Correa et al. (2012a) describe an approximately 20 km² field of *Enallopsammia-Lophelia* coral ridges at the base of the Miami Terrace, Straits of Florida, at 630–870 m depth, with more dense coral framework on current-facing flanks and summits. The same coral association is present in the CWC mound province at the toe of the Great Bahama Bank (Correa et al., 2012b). Interestingly, there is only a low abundance of associated megafauna in the Campeche CWC province, a common element of the coral framework associated community elsewhere. For instance, except *Aphrocallistes* sp. and few *Keratoisis* sp., no large suspension-feeding megabenthos was observed during the three ROV dives.

Regarding the structure-forming CWC from the Campeche Bank on a wider perspective, this newly found CWC province is located at a key position, namely at the beginning of the Loop Current that passes over the well-known CWC occurrences of Louisiana and West Florida before it becomes the Florida Current flowing through the Straits of Florida. North of the Straits of Florida the Florida Current forms 90% of the Gulf Stream, passing north along the margins of South Carolina and Georgia, from where also large CWC provinces have been reported (Ross, 2007; Ross and Quattrini, 2007; Messing et al., 2008). South of the Campeche CWC province, *Lophelia* is known

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from off Brazil, Venezuela and Colombia and was recently mapped off Roatan, Honduras (Reyes et al., 2005; Lutz and Ginsburg, 2007; Arantes et al., 2009; Mangini et al., 2010; Etnoyer et al., 2011), thus, following the path of the northward flowing AAIW that bypasses the Campeche Bank (Merino, 1997). Such an oceanic intermediate water gateway (sensu Henry, 2011) may exert strong control on coral larval dispersal routes as has been documented for *Desmophyllum dianthus* populations in the South Pacific (Miller et al., 2011).

5.2 Environmental control on the Campeche cold-water coral ecosystem

The known ranges of temperature (4–13.9°C; Roberts et al., 2006; Freiwald et al., 2009), salinity (31.7–38.8; Freiwald et al., 2004; Davies et al., 2008), dissolved oxygen (2.7–7.2 mL L⁻¹; Dodds et al., 2007; Davies et al., 2008, 2010) and other physico-chemical parameters defining the ecological niche of *L. pertusa* in the NE Atlantic (see summary in Davies et al., 2008) are found in many parts of the world's oceans (Davies and Guinotte, 2011). Water mass properties obtained for the Campeche margin, such as temperature (9.5–7.5°C) and salinity (35.1–34.9), fit well into these defined thresholds (Fig. 7). The observed content of dissolved oxygen of ~ 2.7 mL L⁻¹ matches observations from the Viosca Knoll area in the northern Gulf of Mexico, where *Lophelia* colonies currently thrive at the lowest reported oxygen levels of 2.7–2.8 mL L⁻¹ (Davies et al., 2010). It is assumed that these extreme oxygen conditions cause decreased growth rates or even inhibits reproductive processes (Brooke and Young, 2003).

However, despite a suited physico-chemical setting, the presence of suitable hardgrounds for the corals to settle on, and even more important, the availability of sufficient food is crucial for the establishment and long-lasting development of a vivid CWC ecosystem. In general CWC feed on fresh phytodetritus (Duineveld et al., 2004, 2007; Kiriakoulakis et al., 2005), on zooplankton (Carlier et al., 2009; Dodds et al., 2009) or on a combination of both (van Oevelen et al., 2009). Recent laboratory studies also revealed the importance of dissolved organic matter which might be actively absorbed by CWC especially during periods when particulate food is scarce (Gori et al., 2013).

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of food to the CWC. The depth range of the Campeche CWC is often reached by migrating zooplankton. For instance, off the California coast, a depth of ~ 560 m has been shown to be a preferred depth of the zooplankton to spend the daytime (Plüddemann and Pinkel, 1989). The potential of daily migrating zooplankton as an additional food source for the CWC has also been put forward by Mienis et al. (2012) based on ADCP observations in the Viosca Knoll area in the northern Gulf of Mexico.

6 Conclusions

The Campeche CWC province is one of the largest coherent CWC areas discovered so far, and the most relevant in the western Atlantic Ocean. A healthy and highly diverse CWC ecosystem is developed on top of a complex system of 20 to 40 m high, partly interconnected ridges, which probably can serve as a paleo-environmental archive enabling the reconstruction of the long-term development of the Campeche CWC province over the Late Quaternary climatic cycles.

The location of the Campeche CWC province appears to be almost perfect for the establishment of such a large CWC ecosystem. It is (a) located underneath a local upwelling center providing high primary production, (b) influenced by a very dynamic bottom current regime delivering food particles to the corals, and (c) characterized by a physico-chemical setting that fits the recognized ecological needs of *L. pertusa*. The observed diel vertical migration of zooplankton possibly reaching the intermediate depth of the CWC ecosystem may even serve as a supplemental food source as already indicated by Mienis et al. (2012). These observations fits several paleo-environmental studies, highlighting the controlling role of the food supply on the long-term development of such ecosystems (Dorschel et al., 2005; Wienberg et al., 2010; Eisele et al., 2011; Fink et al., 2013).

In many places in the world oceans the physico-chemical setting comply with the niche requirements of *L. pertusa* and other CWC (Davies and Guinotte, 2011), however, only in some of these places CWC ecosystems have developed. Thus, the

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Campeche CWC province appears to be an excellent example showing that food supply – controlled by a variety of mechanisms – plays a major role in the development of CWC ecosystems.

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Table 1. Metadata of CTD casts and ROV CHEROKEE video surveys conducted at the Campeche cold-water coral province during R/V *Maria S. Merian* cruise MSM20-4. Abbreviations: WD water depth.

Station [GeoB-N°]	Gear	Date [2012]	UTC [hh:mm]	Latitude [N]	Longitude [W]	WD [m]	Remark
16303-1	CTD	21 Mar	14:59	22°00.98′	86°02.95′	1246	sound velocity profile
16305-1	CTD	22 Mar	05:21	23°49.87′	87°12.27′	506	sound velocity profile
16316-1 to 16316-13	Yoyo CTD	Start: 24 Mar	00:20	23°51.51′	87°12.12′	576	hourly casts over ~ 12 h; ADCP data were recorded simultaneously over ~ 13 h
		End: 24 Mar	12:01	23°51.52′	87°12.13′	558	
16307-1	ROV	Start: 22 Mar	13:51	23°40.83′	87°10.03′	547	video observation
		End: 22 Mar	16:20	23°50.49′	87°10.71′	577	
16312-1	ROV	Start: 23 Mar	14:31	23°50.35′	87°11.76′	523	video observation
		End: 23 Mar	18:31	23°52.52′	87°12.49′	531	
16317-1	ROV	Start: 24 Mar	13:37	23°51.12′	87°12.53′	555	video observation
		End: 24 Mar	15:02	23°51.77′	87°12.16′	556	

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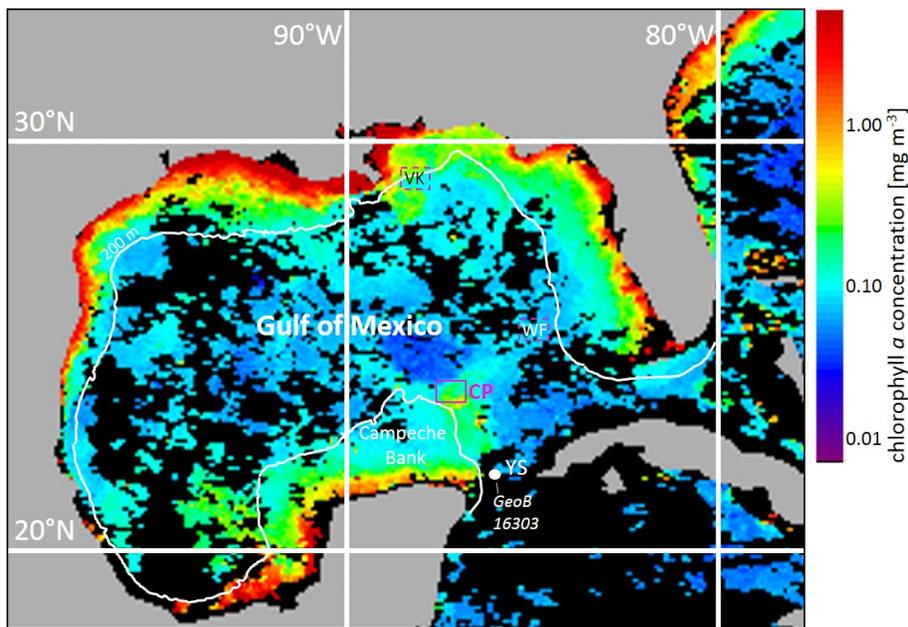


Fig. 1. SEAWIFS satellite ocean color data transferred into chlorophyll *a* concentrations for the Gulf of Mexico (source: <http://oceancolor.gsfc.nasa.gov>). Black indicates data gaps. The map refers to an 8 days composite representing the period 22–29 September 2010. The Campeche cold-water coral province (CP) is influenced by increased productivity probably forced by local upwelling at the northeastern rim of the Campeche Bank (Molinari and Morrison, 1988). The white dot in the Yucatan Strait (YS) indicates CTD station GeoB 16303-1. The white line marks the 200 m isobath within the Gulf of Mexico. VK: Viosca Knoll cold-water coral setting (e.g., Brooke and Schroeder, 2007), WF: West-Florida cold-water coral mounds (Newton et al., 1987).

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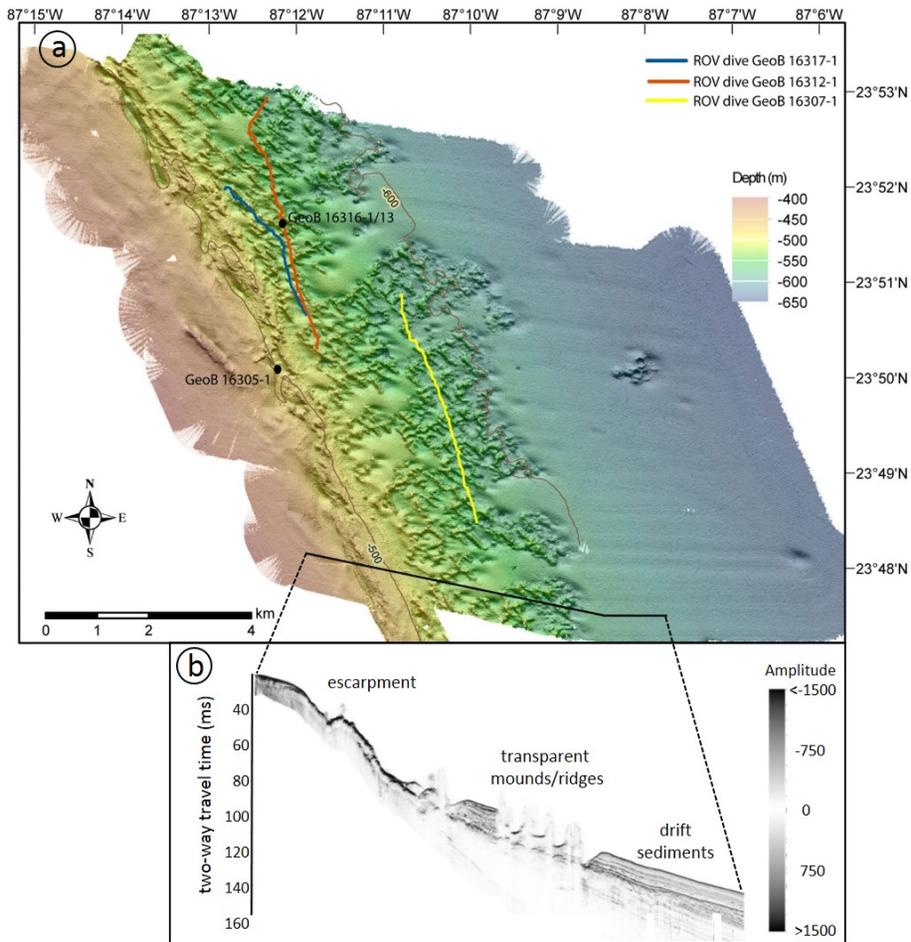


Fig. 2. Caption on next page.

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Fig. 2. (a) Detailed bathymetric map showing the eastern margin of the Campeche Bank comprising the Campeche cold-water coral province revealing numerous individual coral ridges located mainly between 500 m and 600 m water depth. Indicated are CTD sites (black dots) and ROV dive tracks (colored lines; GeoB station numbers are indicated) conducted during R/V *Maria S. Merian* cruise MSM20-4 (for detailed site information see Table 1). **(b)** PARASOUND profile crossing the slope and highlighting the main morphological units.

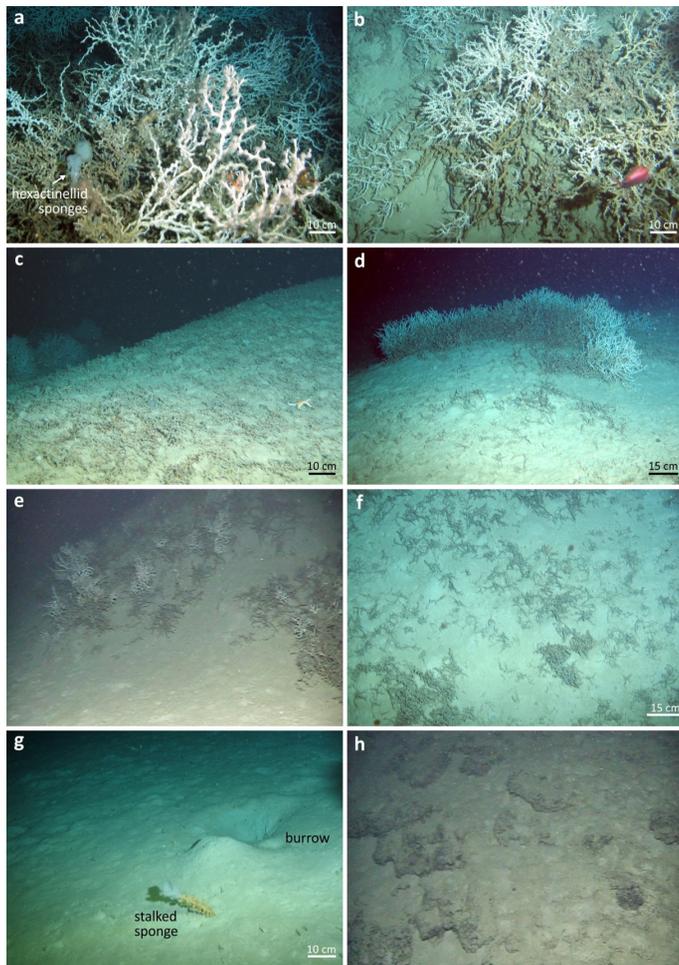


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Fig. 3. ROV images showing the variety of facies types observed for the Campeche cold-water coral province (images copyright MARUM, Bremen, ROV CHEROKEE Team). **(a)** Coral ridge summit: dense colonies of *Lophelia pertusa*, note hexactinellid sponges (*Aphrocallistes* sp.) and squat lobster, **(b)** current-exposed coral ridge flank: ensemble of the fragile *Enallopsammia profunda* and the *brachycephala* morphotype of *L. pertusa*, **(c)** ridge flank packed with dead coral framework, **(d)** arcuate *E. profunda* thicket on a low-relief ridge, **(e)** sudden facies change from flat soft sediment plain to steeply inclined coral ridge flank, **(f)** lower coral ridge flank: dispersed fragments of *E. profunda*, **(g)** interridge area: strongly bioturbated soft sediment, note stalked sponge (*Hyalonema* sp.) colonized by actinarians, **(h)** occasionally observed outcrop carbonate crusts.

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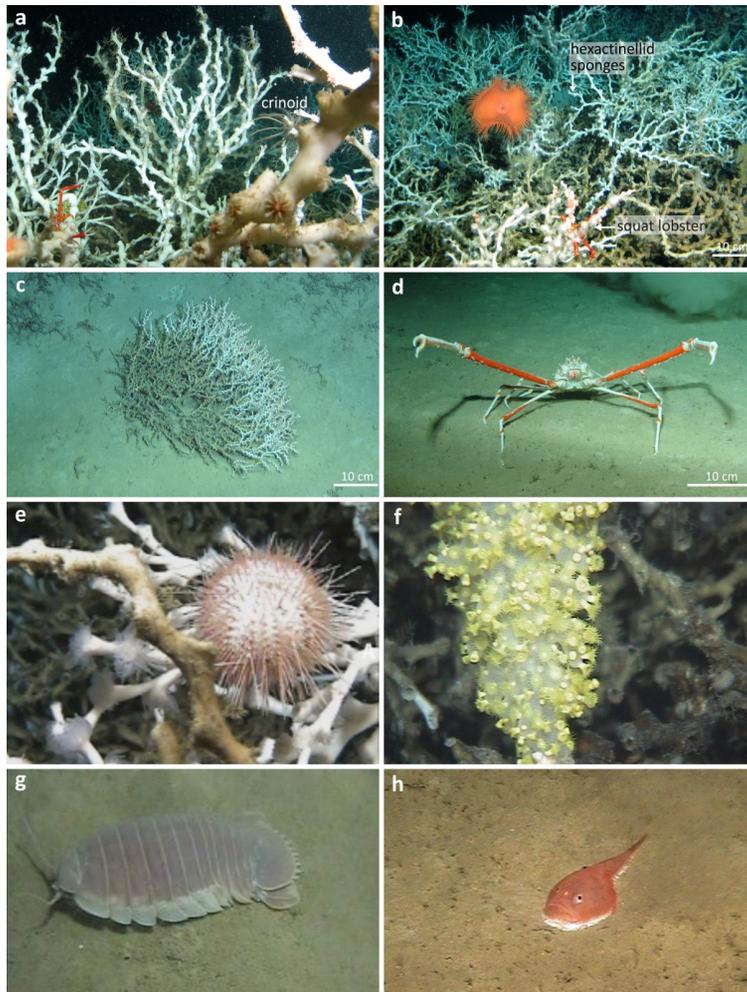


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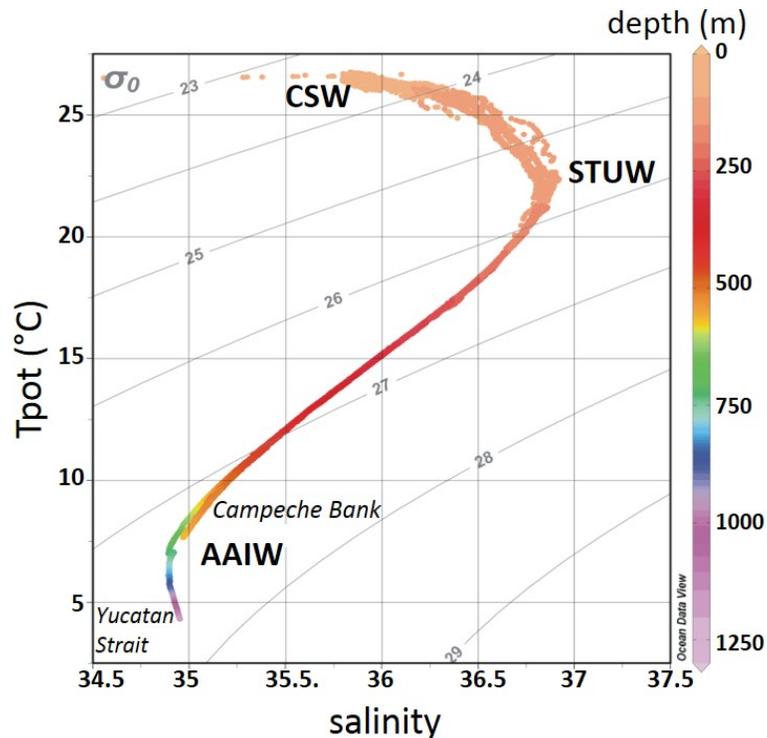


Fig. 5. Water mass structure in the Yucatan Strait (GeoB 16303-1) and in the Campeche cold-water coral province (GeoB 16316-1 to -16, Yoyo-CTD station; see Table 1). Shown is a temperature-salinity plot, temperature is displayed as potential temperature (Tpot), grey lines indicate levels of isodensity (σ_0) in kg m^{-3} (plotted using Ocean Data View v.4.5.1; <http://odv.awi.de>; Schlitzer, R., 2012). Abbreviations: CSW Caribbean Surface Water, STUW Subtropical Intermediate Water, AAIW Antarctic Intermediate Water.

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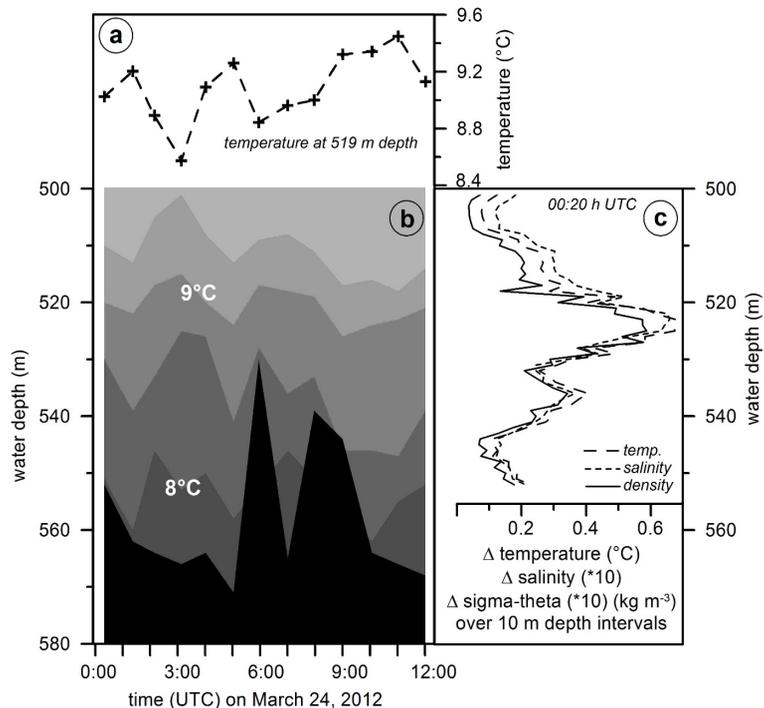


Fig. 6. Hydrological variability below 500 m water depth derived from the Yoyo-CTD station GeoB 16316 (see also Table 1 and Fig. 1). **(a)** Water temperature in 519 m depth measured over a time interval of 12 h (comprising 13 individual CTD casts) indicates a variability of up to 1 °C. **(b)** Depth variation of the 8 °C to 9.5 °C isotherms (grey coloring) over the same time period show partly vertical movements of > 20 m. Variations in water depth (black) are caused by slight movements of the vessel during the Yoyo-CTD station (including the crossing of one CWC ridge). **(c)** Gradients in temperature, salinity, and density over 10 m depth intervals. Data were obtained during the individual CTD cast GeoB 16316-1 (00:20 UTC) and reveal particularly strong gradients around 520 m water depth.

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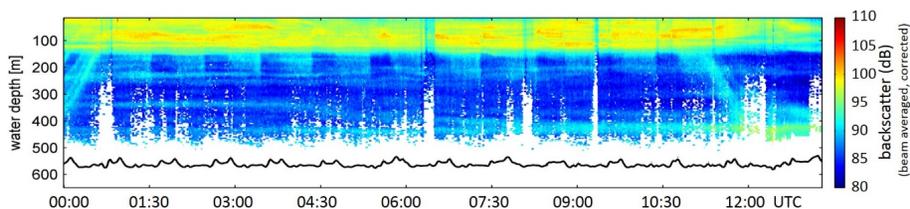


Fig. 7. ADCP-derived backscatter data obtained during a 13h stationary measurement from 0:00 to 13:00 UTC on 24 March 2012. ADCP data were recorded simultaneously to the Yoyo-CTD station GeoB 16316 (see Table 1). This backscatter record shows the upward (0:00–0:30 UTC, local sunset) and downward (11:30–12:00 UTC, local sunrise) migration of the zooplankton. Probably biased data close to the seafloor have been omitted.

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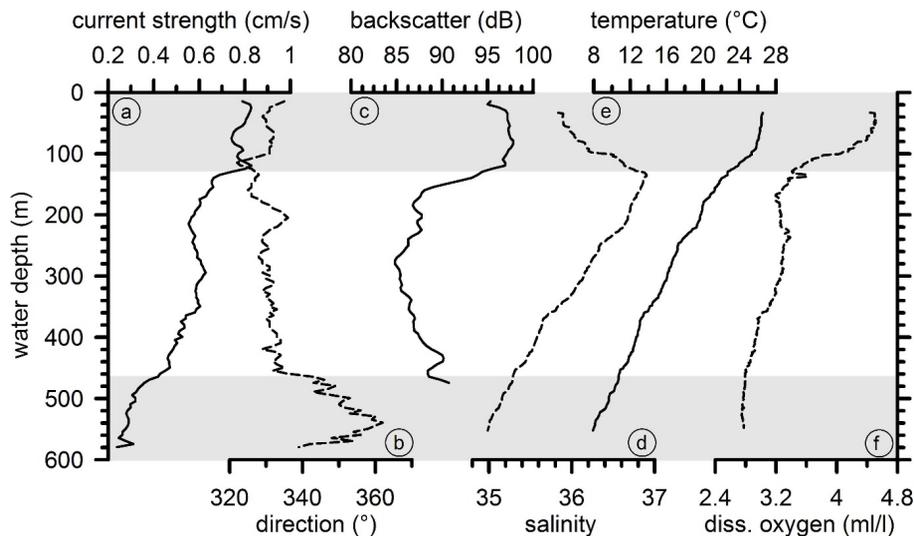


Fig. 8. Water column data for the Yoyo-CTD site GeoB 16316. Mean values for **(a)** current strength, **(b)** current direction, and **(c)** backscatter averaged from the 13h stationary ADCP measurement. CTD-data from cast GeoB 16316-1 for **(d)** salinity, **(e)** temperature, and **(f)** dissolved oxygen. The dashed lines refer to the lower x-axes. The grey shadings delineate the different layers of the water column as derived from the ADCP data.

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