Tidal Dynamics Control on Cold-Water Coral Growth: A High-Resolution Multivariable Study on Eastern Atlantic Cold-Water Coral Sites

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Cold-water coral (CWC) communities form complex benthic ecosystems in a distinct part of the water column. The exact processes supporting CWC reef growth and changes with time are still partly unsolved. Besides local hydrographic conditions, noticeable interactions of tidal flow with topography have been reported for CWC sites. Recent studies have suggested a tidally driven hydraulic control of flow over topographic features as a driver for local overturning at cold-water coral sites. This mechanism proposed a link between surface productivity and coral growth depths and is a driver of resuspension of the bottom material. Only few studies have concentrated on how these processes vary with the health status and structure of the cold-water coral occurrences.

In this study, we explore the processes over tidal cycles by analyzing in situ stratification, hydrography and velocity data which we then combine with local topography from seven Desmophyllum pertusum (previously Lophelia pertusa) dominated eastern Atlantic CWC sites, from the Arctic to the southern hemisphere. The “quality” of CWC sites varies from thriving to declining and dead reefs. We show that living and healthy corals are concentrated at sites, where local hydrodynamics create overturning and mixing which overcomes on a daily basis gravitational particle sinking and thus re-supply food to filter-feeding corals. We find a very wide range of local hydrographic and biogeochemical conditions at the sites which suggests they play only a secondary role for CWC health.

Keywords: cold-water corals, Desmophyllum pertusum, tidal dynamics, food availability, coral growth, hydrodynamics, ecological interactions

INTRODUCTION

Cold-water coral (CWC) communities form complex ecosystems on topographic highs, on continental shelves and on the upper-slope of continental margin (Frederiksen et al., 1992). The reef-scale mechanisms driving their distribution and growth are yet not fully understood. One theory to explain CWC framework initiation and development is the so-called “environmental
control theory” (Roberts et al., 2009), which assumes that the favorable environmental conditions control the distribution and growth of the CWCs. A variety of favorable conditions have been proposed based on the local hydrological and biogeochemical characterization (e.g., oxygen, carbon chemistry, nutrients, temperature, salinity, density and stratification) of the sites (Dodds et al., 2007; Davies et al., 2008; Dullo et al., 2008; Freiwald et al., 2009; White and Dorschel, 2010; Flögel et al., 2014b) as well as food supply, controlled by surface productivity (White et al., 2005; Duineveld et al., 2007). Other studies found CWC occurrence is linked to local topography-bottom flow interactions (Genin et al., 1986; Frederiksen et al., 1992; Miens et al., 2007; Davies et al., 2009; Rüggeberg et al., 2011; Van Haren et al., 2014). Even though most of the thriving CWCs have been found within aforementioned “favorable” conditions it is interesting to note that some thrive in apparently “non-favorable” conditions when considering one specific parameter e.g., in waters with low pH (Georgian et al., 2016b; Baco et al., 2017; Gómez et al., 2018) or with reduced oxygen (< 1 ml l⁻¹) (Hanz et al., 2019). It is assumed that CWC can cope with environmental stress caused by single parameter non-favorable conditions but require higher energetic effort to maintain their functioning (Diaz and Rosenberg, 1995; McCulloch et al., 2012; Sokolova et al., 2012). These sub-optimal sites are however, found in areas with high primary production and it has been suggested that high quality food may compensate the extra necessary energy for CWCs to survive under environmental stress (Cohen and Holcomb, 2009; Georgian et al., 2016b; Hanz et al., 2019). The availability of food has been linked to the physiological performance [e.g., calcification and respiratory metabolism (Naumann et al., 2011; Larsson et al., 2013; Baussant et al., 2017)] and condition (fitness) of corals (Büscher et al., 2017). Other experimental studies have shown no feeding effects in low pH conditions (Maier et al., 2016; Büscher et al., 2017; Gómez et al., 2018) which suggests that CWC populations may prefer different optimal environmental ranges and that CWCs are able to recover from short-term stress, but exposure to long-term unfavorable conditions may increase coral mortality (Dodds et al., 2007; Lunden et al., 2014).

Most dominant reef-forming CWC species like Desmophyllum pertusum (previously Lophelia pertusa) (Addamo et al., 2016) and Madrepora oculata are filter feeders that can feed on a range of organic matter sources such as phytoplankton (Davies et al., 2009), zooplankton (Naumann et al., 2011) or a combination of both (Van Oevelen et al., 2009, 2018; Maier et al., 2019). The source of the food particles lies in near-surface primary productivity layers (Duineveld et al., 2004; Kiriaoulakis and Wolff, 2005; Cathalot et al., 2015) in zooplankton swimming depths or in bottom layers, where the usable carbon content in re-suspended material might be very low due to microbial activity in the benthic layer (Ritzrau et al., 1997; Davies et al., 2009). Laboratory experiments by Orejas et al. (2016) and Purser et al. (2010) have shown efficient prey capture by corals at low flow rates (for zooplankton at flow rates < 2.5 cm s⁻¹ and for phytoplankton < 7 cm s⁻¹). This differs from in situ observations, where CWCs are associated with high flow speeds of > 20 cm s⁻¹ (Mortensen et al., 2001; Thiem et al., 2006; White and Dorschel, 2010) and high tidal activity (Miens et al., 2007, 2012, Davies et al., 2009, 2010). The highest polyp extension rate is seen when hydrographic conditions and flow velocities change due to, e.g., tidal influences both in laboratory (Mortensen, 2001) and in situ experiments (Johanson et al., 2017). In the latter case, the highest polyp activity is seen a couple of hours after high tide (Johanson et al., 2017).

The hydraulics controlling food supply have got more attention during recent years. A link between primary productive surface and CWC depths can be formed by hydraulic control of stratified flow over topographic features such as mounds, sills, escarpments, canyons, etc. This kind of topographic feature generates disturbances in flow and water-column stratification (Soetaert et al., 2016). The processes include for example internal waves and local up- or downwelling (Pratt, 1986; Dewey et al., 2005; Jackson et al., 2012). The first sub-basin scale studies aiming to include the interaction between internal tides and topography in relation to the abundance of suspension- and filter-feeders were published in the early 1990s by Rice et al. (1990) and Farmer and Armi (1986). Today, the tidally driven hydraulic control of stratified flow over topographic features has been identified both with observations (White, 2007; Davies et al., 2009; Findlay et al., 2013; Cyr et al., 2016) and simulations (Mohn et al., 2014; Soetaert et al., 2016) as the major driver for oscillation of water mass interface that creates periodically varying living conditions and vertical mixing at CWC reefs.

The stratified flow is under hydraulic control when it is forced to transition from subcritical to supercritical flow (Armi, 1986; Findlay et al., 2013). This transition can be described by the dimensionless Froude number, Fr = U/c_0. It represents the ratio of the speed with which advection and wave propagation carry information of a disturbance throughout a system (Mayer and Fringer, 2017). Small (Large) Fr represents subcritical (supercritical) flow. When Fr becomes close to 1, the flow is under hydraulic control. Several Fr estimations have been used to estimate the hydraulic control of flow or the topographic blocking at CWC sites (Davies et al., 2009; Mohn et al., 2014; Cyr et al., 2016). The previous estimations have not, however, captured both the near-seafloor stratification or water mass boundaries (White and Dorschel, 2010; Hebbeln et al., 2014) and the oscillating nature of the bottom flow.

Previous studies that link hydrodynamics and CWC reef growth and distribution have focused on thriving CWC communities on high (> 100 m) CWC mounds on the Irish margin (Frederiksen et al., 1992; Davies et al., 2009; Mohn et al., 2014; Cyr et al., 2016). CWCs are found, however, globally from the tropics to the polar regions (Freiwald et al., 2017) and they grow on a variety of morphological structures. CWC occurrences vary from single colonies to large frameworks (Davies et al., 2017). Flögel et al. (2014b) have shown that this difference in quality of CWC sites is linked to distinct oceanographic and hydrographic settings. One aspect of this study is to investigate whether the hydraulic control is important for CWC sites in all qualities on basin scale or whether it is only characteristic for NE Atlantic thriving CWC reefs.

To better understand the impact of varying ocean dynamics on CWC habitats, we use high-resolution physical, biogeochemical, and ecosystem data from seven CWC sites on the eastern margin.
of the Atlantic, from the sub-arctic to the subtropical southern hemisphere (Figure 1). We use observations from a wide range of hydrographic and hydrodynamic settings. To distinguish between different health states of CWC sites, we employ a categorization following Flögel et al. (2014b). The chosen sites are dominated by the scleractinian reef-forming coral *D. pertusum*. Multi-variable lander studies have previously been used in single locations e.g., in the Gulf of Cadiz (Mienis et al., 2012), Bay of Biscay (Dullo et al., 2018) and coastal Scotland (Davies et al., 2009) but they have never been applied to an eastern Atlantic North-South transect.

**REGIONAL SETTINGS OF THE SITES**

The seven studied CWC sites are located along the eastern Atlantic from the sub-arctic into the subtropical southern hemisphere within three areas: near-shore Norway (two sites), the western European Atlantic margin (three sites) and southwestern African margin (two sites) (Figure 1). These regions have characteristic water masses and ocean currents that set up the large scale boundary conditions for the CWC distribution and growth. The morphological structures vary from mounds and sills (four sites) to ridges and escarpments (three sites). In order to compare the effect of the distance from the living corals on hydrography and on flow, we add one subsite in the vicinity of a CWC sill on a sea-floor without corals as a reference site (Figure 2).

To distinguish the thriving and healthy CWC sites from declining and dead ones, we use a categorization based on ROV video and still-photo footage following Flögel et al. (2014b). The sites are classified into four categories based on the coral growth density and the vertical and horizontal dimensions of the CWC framework and coral growth. Category I represents the healthy CWC reefs and mounds with significant vertical (> 1 m) and horizontal (> 100 m²) CWC growth dimensions. The living colonies dominate (> 2/3 of coverage) over the dead ones and the colonies have several living generations. In the case of CWC mounds, the coral framework can be up to several 100s meters high. Three of the studied sites belong to this category (Table 1). Smaller but healthy CWC sites belong to category II (Table 1), where corals have patchier growth pattern with colonies of some square meters and limited vertical elevation. One of the studied sites belongs to this category. Category III sites (Table 1) are dominated by dead CWC framework with only small and isolated living CWC colonies. One of the sites belongs to this category. Two of our sites do not have any living CWCs but only dead CWCs and coral rubble, and thus belong to category IV (Table 1).

**Hydrography of the Sites**

CWC reefs are usually found below the surface waters at intermediate water depths (200–1000 m), but the absolute growth depth of CWCs can vary between 40 and 3000 meters (Freiwald and Roberts, 2005). Therefore, we concentrate here on those water masses that are relevant to CWCs and ocean currents linked to them (Emery, 2003).

The waters off Norway are characterized by the Norwegian Coastal Water (NCW), which is a mixture of saline Atlantic Water (AW) carried to the area via the North Atlantic Drift (NAD) and fresh water input from rivers, the North Sea runoff and the Baltic Sea. NCW is dominant water mass in the northward flowing Norwegian Coastal Current (NCC). The cold, fresh, and oxygen-rich seasonal Winter Mode Water (WMW) forms during the winter and is usually present in between the surface waters and the NCW from spring to autumn (Sætre and Ljøen, 1971; Mork, 1981).

The water masses along the western European Atlantic margin are predominantly of North Atlantic and Mediterranean origin (Pollard et al., 1996). Below the surface waters, the uppermost water mass is the Eastern North Atlantic Central Water (ENACW) flowing southwards along the coast (Pingree and Le Cann, 1989). The lower part of the ENACW is laterally influenced by the Eastern Atlantic Subarctic Intermediate Water (EASIW) indicated by a salinity minimum. Below, salinity increases and
oxygen levels drop due to the influence of Mediterranean Outflow Water (MOW). Mediterranean Outflow (MO) flows from the Mediterranean as a contour current (Pingree and Le Cann, 1989; Daniault et al., 1994; Iorga and Lozier, 1999) to the Bay of Biscay toward the north. The deepest water mass below the MOW is the southward flowing North Atlantic Deep Water (NADW).

The southwestern African coast is an eastern boundary upwelling system where upwelling is driven by coastal parallel winds. Upwelling takes place from Cape Agulhas (∼34°S) to the Angola Benguela Frontal Zone (∼15°S) (Hutchings et al., 2009). The upwelled waters in the south and further off-shore are dominated by Eastern South Atlantic Central Water (ESACW). It is mixture of water masses formed in the South Atlantic, namely the South Atlantic Central Water (SACW, Gordon, 1981; Mittelstaedt, 1991; Poole and Tomczak, 1999) and thermocline water that originate from the Indian Ocean and enters the South Atlantic by Agulhas Current intrusions around the South Cape of Africa (Poole and Tomczak, 1999; Mohrholz et al., 2008). The water mass further to the north and more coastal is the low saline, oxygen depleted and nutrient rich Angola Gyre subtype of the SACW. This subtype of the SACW originates in the subtropical Angola Gyre and enters the Namibian margin via the Angola Current (Duncombe Rae, 2005; Mohrholz et al., 2008). The intermediate and deep water masses of the region are the northward flowing cool and fresh Antarctic Intermediate Water (AAIW, Stramma and Schott, 1999) and the NADW beneath it.

**Topography of the Sites**

The northernmost site is located in the Stjernsund in northern Norway. This WNW–ESE oriented sound connects the open North Atlantic with the Altafjord. The main geomorphologic formation within the sound is an asymmetric morainic sill, which hosts one of the northernmost *D. pertusum* reefs (STJ, 70.02°N, 22.02°E, Figures 2B, 3A). The crest depths of the sill vary between 203 m and 236 m. Thriving CWC colonies (category I) cover the sill on the WNW slope between 235 m and 305 m water depths and on the ESE slope between 245 m and 280 m. Living corals have colony thicknesses of 2–8 m on average. The horizontal extent of the CWC complex is up to one square kilometer (Rüggeberg et al., 2011).

Off central Norway, the category I CWC reef at Nordleksa (NL, 63.61°N, 9.38°E, Figures 2C, 3B) is located at the mouth of the Trondheimsfjord. CWCs are growing on a ridge-like formation with a steep N–NW slope. Its summit is at 125 m and base at 300 m water depth. The CWCs cover an area of about 25 m in W–E and about 600 m in N–S direction, with a saddle like depression between the two main reef tops. The living
Juva et al. Tidal Control on CWC Growth

### TABLE 1

| Site             | Lat [°N] | Lon [°E] | CWC cat. | Depth range of CWCs [m] | Lander depth [m] | Deployment period | Study period | Measurement details for lander ADCP and CTD. | SF [min] |
|------------------|---------|----------|----------|-------------------------|-----------------|------------------|-------------|-----------------------------------------------|----------|
| Stjernsund (STJ) | 70.27   | 22.45    | Ref.     | 362–1230                | 245             | 2.6.–31.7.12     | 7.–12.6.12  | 1.6–50.6                                      | 15.00    |
| Stjernsund (STJ) | 70.26   | 22.47    | I        | 235–305                 | 235             | 25.4.–31.9.12    | 7.–12.6.12  | 6.2–111.2                                     | 10.00    |
| Nordleksa (NL)  | 63.61   | 9.38     | I        | 145–210                 | 210             | 14.–20.6.14      | 7.–12.6.12  | 6.16–122.16                                   | 1.00     |
| Galway Mound (GM)| 51.46   | −11.75   | I        | 850–950                 | 860             | 14.–20.6.11      | 7.–12.6.12  | 6.16–122.16                                   | 1.00     |
| St. Nazaire Canyon (SNC) | 46.23 | −4.33 | III       | 700–850                | 830             | 19.–26.11.16     | 19.–26.11.16 | 6.16–122.16                                   | 1.00     |
| Pagés Escarpment (PE) | 44.04 | −5.71 | IV        | 160–255                 | 228             | 19.–26.11.16     | 19.–26.11.16 | 6.16–122.16                                   | 0.17     |
| Valentine Mound (VM) | 9.73  | 12.73   | II       | 330–470                 | 433             | 19.–26.11.16     | 19.–26.11.16 | 6.16–122.16                                   | 5.00     |
| Sylvester Mound (SM) | −20.75 | 12.73  | IV        | 160–255                 | 228             | 19.–26.11.16     | 19.–26.11.16 | 6.16–122.16                                   | 5.00     |

**FIGURE 3** In situ photographs of CWC sites: (A) Stjernsund, dense living *D. pertusum* colonies with sponges (Freiwald and Dullo, 2014), (B) Nordleksa, living *D. pertusum* colonies with sponges (Form et al., 2015), (C) Galway Mound, dense CWC reef,© MARUM University of Bremen, (D) St. Nazaire Canyon, single coral colonies, (E) Pagés Escarpment, coral rubble, (F) Valentine Mounds, living *D. pertusum* colonies (mound top) with sponges © MARUM University of Bremen (2016), (G) Sylvester Mound, dead coral framework with dense colonization of yellow bryozoans, actinarians and sponges © MARUM University of Bremen (2016).

Coral colonies (category I) cover the southern flank of the mound densely from 850 m to 950 m water depth. Thriving CWC colonies (category I) cover the southern flank of the mound densely from 850 m to 950 m water depth (Dorschel et al., 2007). In the northern Bay of Biscay, the Armorican margin is characterized by a broad shelf with a steep slope. It is
characterized by numerous spurs and canyons among which the St. Nazaire Canyon (SNC, 46.23°N, 4.33°W, Figures 2E, 3D) is a prominent one. This almost N–S oriented canyon has W–E oriented spurs. Living scleractinian colonies (category III) are mostly found on ridges within a depth range of 700–850 m. They are isolated and few in number compared to the dead CWCs. Not far distal from the crest of the ridges the corals are already covered by sediments. The studied ridge is on the eastern side of the canyon, SW–NE oriented approximately 3 km long and 0.5 km wide. It rises approximately 200 m above its surroundings (Flögel et al., 2014a).

In the southern Bay of Biscay, west of the Le Danois Bank on the Cantabrian Margin, the Pagés Escarpment (PE, 44.04°N, 5.71°W, Figures 2F, 3G) rises steeply from 2000 m to 260 m (Dullo et al., 2018). The northern summit is at 680 m and base is at 1030 m while the southern escarpment rises to 260 m and has its base is at 750 m water depth. Only D. pertusum rubble (category IV) is found in water depths of 714–865 m. Anthropic impact is significant in this area (Flögel et al., 2014a).

On the Angolan margin, healthy CWC reefs dominated by D. pertusum are found on the top of mounds at water depths between 330 m and 470 m whereas single colonies are found 250–500 m water depth. The studied mound (VM, 9.73°S, 12.73°E, Figures 2G, 3F) is part of the Valentine Mounds cluster. It is SW–NE oriented and rises from 503 m to 413 m. Coral patches dominated by D. pertusum (category II) are found from the summit to 473 m water depth. The coral patches are 2–3 m wide and < 1 m high with living colony thickness < 0.3 m. Additionally, individual colonies are found from 473 m depth down to the mound base (Hebbeln et al., 2017).

On the northern Namibian margin, the dead CWC mounds are part of a larger geomorphologic setting dominated by a NNW–SSE stretching escarpment. Mounds have a rather circular shape and their heights increase from the south to the north (Hebbeln et al., 2017). Sylvester Mound (SM, 20.75°S, 12.82°E, Figures 2G, 3F) is part of the CWC mound cluster west of the escarpment. Mounds occur at a narrow water depth interval ranging from 219 to 246 m and they are 3–12 m high. Only D. pertusum coral rubble (category IV) is covering this 10 m high mound (Hebbeln et al., 2017).

**MATERIALS AND METHODS**

Data used in this study have been collected on nine cruises with RV Meteor (M) and RV Poseidon (POS) over the years 2004–2016. Data are from eight different locations at seven sites (Figures 1–3 and Table 2).

**Sampling**

The main instrumentation used were sea-floor monitoring lander systems instrumented with physical and biogeochemical sensors (Table 1). During deployment and recovery of these bottom landers, local water column temperature, salinity, oxygen as well as local topography were surveyed with the ship (Table 2). Accuracy and sensitivity of the ship-borne instruments are shown in Table 3. The temporal variability at the sites was recorded with instrumentation mounted on bottom landers (Tables 1, 2). Upward looking Acoustic Doppler Current Profiler (ADCP, Table 3) recorded currents from about 2 to 120 m above the sea floor, with common range for all deployments of from 8 to 35 m above the sea floor (Table 3). The additional biogeochemical sensors varied from deployment to deployment. Therefore, only the data derived from the ADCP and CTD measurements is included in this study.

**Cruises and Deployments**

The sites of near-shore Norway are in the Stjernsund (subsites STJ$_S$ and STJ$_P$) and at Nordleksa (NL). At the STJ, two subsites were studied: STJ$_S$ on the top of the sill, where one lander was deployed at 234 m water depth and STJ$_P$ on the NW slope of the sill as a non-coral reference site at 362 m water depth (Figure 2B). Landers were deployed from the spring to the end of the summer 2012 [cruises POS434 (Pfannkuche, 2012a) and POS438 (Pfannkuche, 2012b)]. At NL, a lander was deployed on the reef saddle at 175 m water depth. During the deployment, from summer 2013 to summer 2014 [cruises POS455 (Form et al., 2014) and POS473 (Form et al., 2015)], the lander moved horizontally 100–200 m due to strong currents. The data used in this study were taken from an interval of 87 days when the lander was stable at 210 m water depth (Figure 2C).

The three sites on the western European Atlantic margin are Galway Mound (GM), St. Nazaire Canyon (SNC) and the Pagés Escarpment (PE). At GM, the lander was deployed at 804 m water depth (Figure 2D) from the spring to the autumn 2004 [cruises M61 (Pfannkuche et al., 2004) and POS316 (Pfannkuche and Utech, 2005)]. In the Bay of Biscay, data at sites SNC and PE were collected during June 2011 during cruise M84-5 (Flögel et al., 2014a). At SNC the lander was deployed on a ridge at 806 m water depth for 5 days (Figure 2E) and at PE on the northern side of the escarpment at 776 m water depth for 3.5 days (Figure 2F).

The two sites off the southwestern African coast are the Valentine Mounds (VM) off Angola and the Sylvester Mound (SM) off Namibia (Hanz et al., 2019). They were studied during January 2016 during cruise M122 (Hebbeln et al., 2017). The lander was deployed west from VM at 430 m water depth for 7 days (Figure 2G) and at the southeastern base of SM at 222 m water depth for 14 days (Figure 2H).

**Data Preparation**

For subsequent data analysis, the raw CTD and ADCP data were converted. CTD data were converted to absolute salinity ($S_A$), conservative temperature ($\Theta$), potential density ($\rho$) and potential density anomaly ($\delta\rho$) i.e., sigma-theta values (McDougall and Barker, 2011). The current measurements were corrected for the local magnetic declination based on IGRF-11 model data (Finlay et al., 2010). The echo intensity was converted to mean volume backscatter ($Sv$) (Deines, 1999). This is used as an indicator for the abundance of particles in the water column. The horizontal velocity components (eastward, $u_e$, and northward, $u_n$) were rotated using variance ellipses (Lilly, 2017). Accordingly, the mean direction velocity components ($u_m$) are in the direction of the most energetic fluctuations while components
TABLE 2 | Metadata for CTD casts, ROV and submarine dives and lander deployments.

| Station No. | Gear             | Date       | Time (UTC) | Lat [°N] | Lon [°E] | WD [m] | Remark     |
|-------------|------------------|------------|------------|----------|----------|--------|------------|
| M61/233     | CTD              | 24.4.04    | 11:49      | 51.4503  | −11.8158 | 1066   |            |
| M61/245     | LANDER           | 25.4.04    | 16:26      | 51.4547  | −11.7538 | 806    | Deployment |
| M61/550     | ROV              | 5.6.04     | 9:41       | 51.4610  | −11.7722 | 899    |            |
|             |                  |            | 20:45      | 51.4586  | −11.7559 | 892    |            |
| POS316/606  | LANDER           | 10.8.04    | 10:00      | 51.4633  | −11.7517 | 921    |            |
| POS325/484  | JAGO submarine   | 31.7.05    | 12:14      | 70.2648  | 22.4602  | 319    | Dive #912  |
|             |                  |            | 16:38      | 70.2605  | 22.4622  | 305    |            |
| M84/M579    | ROV/OFOS         | 5.6.11     | 13:43      | 44.075   | −5.68    | 1069   | Dive #3-4  |
| M84/M580    | LANDER           | 5.6.11     | 19:52      | 44.044   | −5.707   | 762    |            |
| M84/M598    | CTD              | 7.6.11     | 5:41       | 44.047   | −5.703   | 764    |            |
| M84/M620    | LANDER           | 9.6.11     | 13:55      | 44.047   | −5.707   | 780    |            |
| M84/M624    | LANDER           | 14.6.11    | 5:25       | 46.232   | −4.325   | 814    |            |
| M84/M646    | ROV/OFOS         | 15.6.11    | 2:39       | 46.233   | −4.32    | 660    | Dive #11   |
| M84/M656    | CTD              | 15.6.11    | 20:00      | 46.23    | −4.353   | 1357   |            |
| M84/M692    | LANDER           | 20.6.11    | 6:55       | 46.234   | −4.322   | 760    | Recovery   |
| POS434/145  | CTD              | 1.6.12     | 8:26       | 70.2698  | 22.4452  | 368    |            |
| POS434/147  | CTD              | 1.6.12     | 13:56      | 70.2639  | 22.4925  | 311    |            |
| POS434/151  | LANDER           | 2.6.12     | 16:57      | 70.2702  | 22.4479  | 362    | Deployment |
| POS434/155  | LANDER           | 4.6.12     | 9:45       | 70.2581  | 22.4723  | 235    | Deployment |
| –           | LANDER           | 31.7.12    | 6:55       | 70.2702  | 22.4479  | 0      | Suraced    |
| –           | LANDER           | 10.8.12    | 18:00      | 70.2702  | 22.4479  | 0      | Recovery   |
| POS438/431  | LANDER           | 15.9.12    | 11:10      | 70.2658  | 22.4748  |        |            |
| POS455/837-2 | CTD            | 30.6.13    | 6:35       | 63.6095  | 9.3748   | 236    |            |
| POS455/842-1 | LANDER       | 2.7.13     | 7:12       | 63.608   | 9.38267  | 185    | Deployment |
| POS473/887-1 | JAGO         | 18.8.2014  | 6:57       | 63.6077  | 9.3840   |        | Dive #2    |
|             |                  |            | 11:05      | 63.6083  | 9.383   |        |            |
| POS473/896-1 | LANDER     | 21.8.14    | 9:26       | 63.6088  | 9.3822   |        | Recovery   |
| M122/M001-4 | LANDER          | 1.1.16     | 18:07      | −20.732  | 12.8185  | 222    | Deployment |
| M122/M007-1 | ROV            | 2.1.16     | 9:18       | −20.735  | 12.814   | 246    | Dive #2    |
|             |                  |            | 12:13      | −20.731  | 12.813   | 241    |            |
| M122/M020-1 | CTD            | 3.1.16     | 17:31      | −20.733  | 12.8138  | 247    |            |
| M122/M001-4 | LANDER          | 14.1.16    | 6:37       | −20.814  | 12.8135  | 240    | Recovery   |
| M122/M101-1 | ROV            | 19.1.16    | 11:46      | −9.7278  | 12.7148  | 473    | Dive #9    |
|             |                  |            | 16:21      | −9.7168  | 12.7168  | 426    |            |
| M122/M098-1 | LANDER          | 19.1.16    | 8:28       | −9.7262  | 12.7311  | 430    | Deployment |
| M122/M098-1 | CTD            | 17.1.16    | 17:01      | −9.7291  | 12.7146  | 501    |            |
| M122/M098-1 | LANDER          | 26.1.16    | 5:05       | −9.7262  | 12.7311  | 430    | Recovery   |

WD, water depth.

perpendicular are interpreted as a cross flow ($u_c$). The vertical velocity component, $u_v$, was not altered.

Since the deployment periods varied from 3.5 days to up to more than 1 year, we used 1 week time series where possible and the whole deployment period, where deployment times were shorter than 1 week. The study period of all deployments is sufficient to capture short-term variability such as semi-diurnal internal tides, but we are aware of possible effects of different lengths of the datasets.

**Data Analysis**

The mean conditions around the CWCs are described with the time-averaged mean values and standard deviation (SD) of hydrography and flow time series. For analysis, a 1-h running mean is used to remove higher frequency spikes and outliers (Lilly, 2017).

The site-characteristic dominant tidal frequencies, $\omega$, and their amplitudes, $a$, were analyzed with the harmonic analysis toolbox T_Tide (Pawlowicz et al., 2002). The tidal signals for barotropic and baroclinic tidal signals were analyzed by using bottom pressure and horizontal velocity fields at 8 ($u_8$) and 35 ($u_{35}$) meters above the sea-floor (masf). Only tidal signals with signal-to-noise ratio (snr) > 2 are considered significant.

The effect of near-bottom mean direction velocity ($u_{m,8}$) on hydrography and correlation between flow components was estimated using zero-normalized cross-correlation (ZNCC) analysis. For analysis, the signals were first de-trended, the signal mean was subtracted and the signal was divided by its
TABLE 3 | Instrumentation details and metadata for landers and onboard CTDs.

|                      | Landers                     | CTD RV Meteor               | CTD RV Poseidon             |
|----------------------|-----------------------------|-----------------------------|-----------------------------|
| ADCP                 | RDI Workhorse sentinel 300 kHz or 600 kHz | SBE 9 plus                  | SBE 9 plus                  |
| Velocity acc/res     | 0.5% for 300 kHz, 0.3% for 600 kHz | ± 0.001/0.0002              | ± 0.001/0.0002              |
| Echo intensity acc/res| ± 1.5 dB                    | ± 0.3/0.04                  | ± 0.3/0.04                  |
| CTD                  | SBE 16 plus/RBR XR-420CTm    | SBE 11 plus deck unit       | SBE 11 plus deck unit       |
| T in acc/res [°C]    | ± 0.005/0.0001 or ± 0.002/0.00005 | ± 0.015/0.001               | ± 0.015/0.001               |
| C in acc/res [mS m⁻¹] | ± 0.5/0.05 or ± 0.003/0.001 | ± 0.015/0.001               | ± 0.015/0.001               |
| P in acc/res [% WD⁻¹] | ± 0.1/0.002 or ± 0.05/0.001 (0.015%) | ± 0.15/0.001               | ± 0.15/0.001               |
| Releaser or Deck unit| Video-controlled launcher or K/MT 562 | SBE 11 plus deck unit       | SBE 11 plus deck unit       |
| Additional sensors   | Sediment trap, camera, a single point current meter, SAMS/optical sensors, turbidity, dissolved oxygen, pH, chl-a, fluorescence | Dissolved oxygen, seabird bottle release, Niskin bottle | Fluorescence of chl-a, dissolved oxygen, turbidity, 12 × 10 rosette |

acc, accuracy; res, resolution; T, temperature; C, conductivity; P, pressure; WD, water depth.

standard deviation. Since the sampling interval between the flow and hydrography measurements vary, those time series were interpolated to 10-min sample intervals for the analysis. ZNCC measures the Pearson correlation coefficient, R, between two time series with time delay (τ). When signals are positively (negatively) correlated, the ZNCC function maximum (minimum) indicates the τ where signals are best aligned. With positive (negative) τ the primary variable is leading (lagging) from the secondary variable. The strong and symmetric periodicity of the ZNCC function implies that processes are regular throughout the time series. We used ZNCC with a maximum time lag of 24 h to compare the influence of the mean direction velocity at 8 masf (u8) and 35 masf (u35), and mean direction velocity at 35 masf (u8,35). Only significant (p < 0.001) correlations are presented.

Finally, for hydraulic control estimations we consider the flow around the CWCs to be hydrostatic two-layer flow introduced by Baines and Johnson (2016) with uniform velocity over topographic features. We also take into account the time-varying and stratified nature of the flow (Marshall et al., 1997; Dewey et al., 2005). The topographic effects for this flow can be described in terms of the two-layer Froude number, Fr, topography height ratio, Hm, the layer thickness ratio, r, non-hydrostatic parameter, ε, and excursion number, Ex, where

\[
Fr = \frac{U}{c_0}, \quad \epsilon = \frac{\Delta \rho g}{\rho_1 + \rho_2}, \quad H_m = \frac{h_2}{\rho_1},
\]

\[
r = \frac{h_1}{H}, \quad \epsilon = \frac{U^2}{(\frac{1}{2})\omega^2 N^2}, \quad Ex = \frac{2U}{\omega L}
\]

(1)

where U is the horizontal flow speed, c0 is the speed of long waves in two-layer fluid at rest, ρ1 and ρ2 denote the lower and upper layer densities, Δρ = ρ2 − ρ1, g is gravity, h1 and h2 are the lower and upper layer thicknesses, H = h1 + h2 is the total water depth, bm is the height of the morphologic structure, L is the horizontal length scale i.e., the width of the morphologic structure, N = (ερg/(ρc2))¹/² is the buoyancy frequency used to represent the water column stratification and ω is the oscillating (tidal) frequency. A definition sketch is given in Figure 2A. The Fr−Hm diagram shows parameter ranges where the stratified flow is subcritical or supercritical over the topography, and where the flow is blocked or partially blocked by the morphologic structure (Figure 4; Baines, 1998, 2015; Baines and Johnson, 2016). If the morphologic structure blocks the flow partially and the lower layer is thinner than the upper layer (r < 0.5), hydrostatic flow generates a hydraulic jump. The motion can be considered hydrostatic or quasi-steady, if Ex ≫ 1 (Dewey et al., 2005), and ε ≪ 1 (Marshall et al., 1997). Under these conditions, the advective timescale is larger than the tidal time scale so that the flow experiences the total height of the morphologic structure (Ex ≫ 1) during the tidal cycle but it is smaller than the buoyancy period (ε ≪ 1) so that the non-hydrostatic effects can be neglected. The interaction between the flow and topography should be quasi-steady so that flow disturbances have time to grow and develop.

For the site specific Hm, we can determine lower limit for Fr and hence flow velocity U (when c0 is assumed constant) for partially blocked conditions, Ucr = Fr(Hm) × c0. The development of a significant hydraulic jump requires that the flow supports partially blocked conditions for a period comparable to tcr > L/(2 × Ucr) (Dewey et al., 2005). The vertical displacement scale i.e., the maximum vertical movement of the isopycnals, Δh, is controlled by stratification, flow, the height of the morphologic structure and time and length scales. If the time scale is large (Ex ≫ 1), and the height of the topography (b_m > U/N) or the depth of the fluid (H − b_m > U/N) do not affect the motion, the vertical displacement is Δh = Umean/N (Legg and Klymak, 2008).

RESULTS

Water Column Structure

The CTD casts allow the identification of the regional water masses and their boundaries. The water masses are characterized by their temperature (Θ), salinity (SA) and oxygen (O2) values.
(Figure 5), and their boundaries are found at the stratification \((N)\) maxima (Figure 6). The boundary between water layers \(h_1\) and \(h_2\) is taken at the stratification maximum closest to the summit of the morphologic structure. We include the water column from the surface to the base of the morphologic structure.

At both Norwegian sites, waters are well stratified, cold and oxygen-rich. The seasonal temperature minimum, WMW, is measurable below the surface layer. At site STJ, the WMW is located within the NCW at depths between 100 and 150 m \((\Theta < 5.2^\circ C)\) and at NL above the NCW at depths 40–120 m \((\Theta < 7.6^\circ C)\). At both sites, the NCW occupies most of the water column and the influence of AW is only seen near the bottom with \(S_A > 35 \text{ g kg}^{-1}\) (Figure 5). The CWCs are found in well oxygenated waters \((O_2;\text{CWC} = 6.11-6.21 \text{ ml l}^{-1})\). At NL, the mean stratification is stronger \((N = 7.7 \times 10^{-3} \text{ s}^{-1})\) than at STJ \((STJ_p: N = 4.1 \times 10^{-3} \text{ s}^{-1} \text{ and STJ}_S: N = 4.3 \times 10^{-3} \text{ s}^{-1})\). Below the surface layer, the stratification maximum is at the boundary between the WMW and the NCW \((STJ_p: h_2 = 202 \text{ m}, STJ_S: h_2 = 192 \text{ m}, NL: h_2 = 120 \text{ m})\) (Figures 6A–C).

On the western European Atlantic margin, waters are relatively saline and weakly stratified. The ENACW is found below the surface layer to around 400–550 m, where the salinity minimum \((GM: 35.61 \text{ g kg}^{-1}, SNC: 35.79 \text{ g kg}^{-1} \text{ and PE: 35.77 g kg}^{-1})\) indicates the presence of the EASIW. The salinity maxima and oxygen minima below the EASIW \((GM: S_A = 35.59 \text{ g kg}^{-1}, O_2 = 3.68 \text{ ml l}^{-1}, SNC: S_A = 35.73 \text{ g kg}^{-1}, O_2 = 4.15 \text{ ml l}^{-1} \text{ and PE: } S_A = 35.84 \text{ g kg}^{-1}, O_2 = 3.92 \text{ ml l}^{-1})\) show the presence of the MOW. The cold, fresh and oxygen-rich NADW occupies the waters below the MOW \((\Theta < 8^\circ C, S_A < 35.5 \text{ g kg}^{-1} \text{ and } O_2 > 4.5 \text{ ml l}^{-1})\) (Figure 5). Oxygen concentrations at the depth range of CWCs are lower than at the near-shore Norway \((O_2;\text{CWC} = 3.81-4.24 \text{ ml l}^{-1})\). The mean stratification is weak \((N \approx 2.5 \times 10^{-3} \text{ s}^{-1})\). The deep-layer stratification maximum is found at the boundary between the EASIW and the MOW \((GM: h_2 = 846 \text{ m}, SNC: h_2 = 812 \text{ m}, PE: h_2 = 868 \text{ ml})\). It is strongest at GM followed by SNC and PE (Figures 6D–F).

At sites VM and SM, waters are warm and oxygen-depleted. Below the warm and saline surface waters lies the SACW where oxygen drops to minimum \((O_2 < 1 \text{ ml l}^{-1})\). At site SM, the SACW occupies the remaining water column. At VM, the presence of the AAIW is seen below 580 m with oxygen increase to levels \(O_2 > 1 \text{ ml l}^{-1}\) and temperature drop to \(\Theta < 7^\circ C\) (Figure 5). The oxygen levels at the depth of CWC occurrence are hypoxic \((VM: O_2;\text{CWC} = 0.52 \text{ ml l}^{-1} \text{ and SM: } O_2;\text{CWC} = 0.10 \text{ ml l}^{-1})\). The water columns are well stratified \((VM: N = 5.2 \times 10^{-3} \text{ s}^{-1} \text{ and SM: } N = 5.6 \times 10^{-3} \text{ s}^{-1})\). The maximum stratification around mounds at VM and at SM is found at 328 m and 190 m water depths, respectively (Figures 6G,H).
**Lander Measurements**

The near-seafloor hydrography (Θ, S_A, and σ_θ, Figures 7A,B) and flow velocity measurements (Figures 7C,D) give the mean conditions and short term variations for the respective coral sites. The velocity regimes are shown for 8 masf and 35 masf (Figures 7C,D).

**Hydrography**

The mean bottom water temperature, Θ, varies between 6.10°C and 12.58°C. Water is cool (Θ < 8.5°C) at near-shore Norway (sites STJ_P, STJ_S and NL) and at VM, in between (8.5 and 10.5°C) at GM, SNC and PE and warm at SM (Θ > 10.5°C). The variations in temperature are small (SD_Θ < 0.05°C) at near-shore Norway and at PE in comparison to other sites where temperature variations are up to fivefold as large (SD_Θ = 0.1–0.5°C). The mean bottom salinity, S_A, ranges between 34.91 g kg⁻¹ and 36.04 g kg⁻¹. Water is relatively fresh (S_A < 35.1 g kg⁻¹) at NL and VM, and saline (S_A > 35.7 g kg⁻¹) on the western European Atlantic margin (sites GM, SNC and PE). The salinity variations are small (SD_S_A < 0.02 g kg⁻¹) at STJ_P, GM, SNC and PE compared to the other sites (SD_S_A > 0.035 g kg⁻¹). The mean sigma-theta, σ_θ, varies from 26.63 kg m⁻³ to 27.68 kg m⁻³. Water is less dense (σ_θ < 27.25 kg m⁻³) at NL, VM and SM, compared to the other sites (σ_θ > 27.55 kg m⁻³). The variations in density are small at STJ_P and PE (SD_σ_θ < 0.017 kg m⁻³), in between (SD_σ_θ = 0.023–0.047) at STJ_S, NL, VM, SM and SNC, and large at GM (SD_σ_θ = 0.058 kg m⁻³).

**Flow Characteristics**

The time-averaged horizontal flow speed, U_mean, varies between 1.6–26.1 cm s⁻¹ and 3.2–27.5 cm s⁻¹ at 8 masf and 35 masf, respectively. Flow speeds are weak (U_mean < 5.5 cm s⁻¹) at STJ_P, SNC, and PE, and medium (U_mean = 8–12 cm s⁻¹) at VM, SM, and GM. The flow speed is suitable for feeding (U_max < 14 cm s⁻¹) at STJ_P, SNC, and PE, and high (U_max > 18 cm s⁻¹) at GM and PE. The peak horizontal flow speed, U_max, varies between 5.6–61.2 cm s⁻¹ and 12.4–72.9 cm s⁻¹ at 8 masf and 35 masf, respectively. It is low (U_max < 14 cm s⁻¹) at STJ_P, SNC, and PE, and medium (U_max = 20–40 cm s⁻¹) at NL, VM, SM, and GM. The flow speed is suitable for feeding (U_max < 7 cm s⁻¹ < 10% of the time) at STJ_P, SNC, GM, and PE. The flow direction is controlled by local topography and large scale circulation. The predominant horizontal flow direction at 8 masf is along the sound or fjord axis at the near-shore Norwegian sites (STJ_S and STJ_P: E–ESE, NL: E–ESE). At the other sites it is along the mounds (GM: NNE, VM: ENE) across the escarpment or the ridge (SNC: SE, PE: ESE–SE) or along the continental slope.
Juva et al. Tidal Control on CWC Growth

FIGURE 6 | Water column stratification, N (solid thin line), and sigma-theta, $\sigma_2$ (dash-dot thin line), for (A) STJ$_S$, Stjernsund CWCs; (B) STJP, Stjernsund reference; (C) NL, Nordleksa; (D) GM, Galway Mound; (E) SNC, St. Nazaire Canyon; (F) PE, Pagés Escarpment; (G) VM, Valentine Mound; and (H) SM, Sylvester Mound. The deep layer stratification maximum (dotted thick line) and summit depth of the morphologic structure (dashed thick line) show the depths ($h_1$, $h_2$ and $b_m$) used in the analysis. At STJ$_S$ only one line is shows, because the stratification maximum and the summit depth coincide. Note that the scale of the y-axis varies from the surface to the base depth of the morphologic structure. The displayed ranges are $N = 0-12 \times 10^{-3} \text{s}^{-1}$ and $\sigma_2 = 26-28 \text{kg m}^{-3}$.

(SM: SSW–S). The mean flow direction varies between 8 masf and 35 masf $< 6^\circ$ at STJ$_S$, STJP, NL and VM, around 10$^\circ$ at GM and $< 20^\circ$ at PE and SM. At SNC the flow direction change is largest from SE to NNE. The flow oscillates from the main direction to its opposite direction at all sites.

Tides

Tidal analysis of the pressure records (Table 4) explains 89.7–98.7% of the pressure fluctuations with 3–5 significant constituents. At all sites, the semidiurnal (M2) signal generates largest amplitude and is thus the most significant constituent. At the near-shore Norway, M2 generates an amplitude of 0.91–0.94 dbar, followed by diurnal K1 (0.08–0.12 dbar) signal. On the southwestern European Atlantic margin, the M2 generates the amplitude of 1.30–1.70 dbar followed by K1 (0.12–0.15 dbar) at sites SNC and PE, and M3 (0.02 dbar) at site GM. At VM and SM, the M2 has amplitude of 0.3–0.6 dbar followed by K1 (0.06–0.09 dbar).

The analyses of the tidal constituents from the horizontal velocity records reveal a different picture (Table 4). With 1–5 significant tidal constituents, tidal analysis explains 7.7–89.0 and 4.6–89.3% of the horizontal velocity fluctuations at 8 masf and 35 masf, respectively. Fluctuations at tidal frequencies explain $> 75\%$ of the horizontal velocities at STJ$_S$, 8, 35 and NL$_{35}$, 44–61% at STJP, 8, 35, NL$_{4}$, GM$_{35}$, PE$_{8}$ and VM$_{8,35}$ and $< 15\%$ at SNC$_{8,35}$, PE$_{35}$ and SM$_{8,35}$. The M2 generates amplitudes of $> 20 \text{ cm s}^{-1}$ at STJ$_S$, 8, 35 and NL$_{35}$, 8–10 cm s$^{-1}$ at GM$_{35}$ and VM$_{8,35}$ and $< 5.5 \text{ cm s}^{-1}$ at STJP, 8, 35, SNC$_{8,35}$, PE$_{35}$ and SM$_{8,35}$. It is the most significant constituent at all sites except at GM$_{8,35}$ and SNC$_{8,35}$, where K1 (17.8–22.5 cm s$^{-1}$) and M6 (0.7–1.5 cm s$^{-1}$) are the most significant constituents, respectively.

Cross-Correlation

The hydrographical parameters are not steady, but seem to follow the velocity fluctuations. The density is salinity driven off Norway and temperature driven elsewhere due to the local water masses. To simplify, only cross-correlations with $\sigma_2$ are discussed.

For sites of category I or II (i.e., STJ$_S$, NL, GM and VM) the cross-correlations of $u_m,8$ with $\sigma_2$ and velocity components $u_w,8$ and $u_m,35$ vary from moderate to strong ($|R| > 0.6$) and offsets are relatively small ($|T| < 6$ h) (Table 5). The $u_m,8$ and $u_w,8$ have moderate to strong correlations ($|R| \geq 0.6$) with small offset ($\tau \leq 20$ min). At STJ$_S$, NL and GM strong $u_m,8$ occurs same time as upward velocities and at VM strong $u_m,8$
The changes in the mean direction velocity components at 8 masf and 35 masf happen simultaneously ($R > 0.89\), $\tau = 0$ min) at these sites. The $u_m,8$ and $\sigma_\theta$ have moderate or strong correlation ($|R| > 0.65$) with $|T| < 6$ h. At STJ$_S$ and VM the peak in bottom density is followed by maximum $u_m,8$ values ($\tau = -2.75$ to $-0.5$ h). At GM and NL, the maximum $\sigma_\theta$ values follow the peak $u_m,8$ after $\tau = 4.8$ h and 5.7 h, respectively and coincide with the minimum $u_m,8$ velocities (Figure 8). The changes in flow direction are semi-diurnal at STJ$_S$, NL and VM and diurnal at GM. This drives the variation in hydrography and the acceleration phase of $u_m,8$ and $u_w,8$ the density increases from its daily minimum to a maximum. $\sigma_\theta$ drops to its minimum when the flow turns and relaxes. The maximum density change within one tidal cycle (M2 at STJ$_S$, NL and VM, K1 at GM) is $> 0.1$ kg m$^{-3}$ at all four sites (Figure 7B). When this tidal density change is compared to water column density measurements (Figure 6), the maximum tidal density change corresponds to a vertical isopycnal displacement of 240 m at GM, around 70 m at STJ$_S$ and VM and 30 m at NL.

For sites in category III and IV (i.e., SNC, PE and SM) or for the reference location (STJ$_P$) the cross-correlations of $u_m,8$ with velocity components or sigma-theta are lower than for the category I–II sites (Table 5). At PE, SM and STJ$_P$ $u_m,8$ and $u_w,8$ have weak correlation ($|R| = 0.3$–$0.45$) with lag $|T| \leq 5.4$ h. At SM and STJ$_P$ strong $u_m,8$ is linked to downward or weak upward vertical flow and at PE upward or weak downward vertical flow. At SNC, $u_m,8$ and $u_w,8$ have no correlation ($R = 0.16\), $\tau = -9.33$ h). At SNC and PE, $u_m,8$ and $u_m,35$ have weak or no correlation ($|R| \leq 0.36$ with $|T| \leq 0.5$ h). At STJ$_P$ and SM the correlations between $u_m,8$ and $u_m,35$ are similar to category I–II sites ($R > 0.7$ with $\tau = 0$ min).
Tidal Control on CWC Growth

TABLE 4 | Tidal analysis for bottom pressure and flow record based on the harmonic analysis toolbox T_Tide (Pawlowicz et al., 2002).

| Site  | %    | Tidal constituent (period in hours) |
|-------|------|------------------------------------|
|       |      | K1 (23.93 h) | M2 (12.42 h) | M3 (6.28 h) | M4 (6.21 h) | 2MK5 (4.93 h) | M6 (4.14 h) |
| STJS  | 93.5 | 0.116       | 0.930       | 0.016       | 0.96       | 2.51       |
| p (dbar) | 89.0 | 2.45        | 33.62       | 4.65        |            |
| uθ,8 (cm s⁻¹) | 89.3 | 2.31        | 38.02       | 0.91        |            |
| uθ,35 (cm s⁻¹) | 93.5 | 0.116       | 0.936       | 0.015       | 0.014      |
| STJp  | 54.1 | 0.78        | 4.11        | 0.31        | 2.35       |
| uθ,8 (cm s⁻¹) | 52.5 | 5.24        | 2.48        |            |
| NL    | 89.7 | 0.078       | 0.917       | 0.033       |
| p (dbar) | 60.8 | 22.69       | 3.47        | 1.41        | 3.28       |
| uθ,8 (cm s⁻¹) | 75.2 | 34.533      | 3.451       |
| SNC   | 98   | 0.123       | 1.701       | 0.009       | 0.035      | 0.004      |
| p (dbar) | 7.7  | 0.56        |            |
| uθ,8 (cm s⁻¹) | 4.6  | 0.95        |            |
| uθ,35 (cm s⁻¹) | 95.2 | 22.51       | 8.73        | 3.74       |
| PE    | 98.7 | 0.145       | 1.304       | 0.013       | 0.027      | 0.002      |
| p (dbar) | 44.5 | 0.58        | 2.65        |            |
| uθ,8 (cm s⁻¹) | 7.2  | 3.01        | 0.64        |
| uθ,35 (cm s⁻¹) | 45.3 | 1.26        | 9.48        |            | 0.49       |
| VM    | 97.7 | 0.094       | 0.530       | 0.006       | 0.006      | 0.002      |
| p (dbar) | 46.8 | 1.26        | 9.48        |            |            |
| uθ,35 (cm s⁻¹) | 92.3 | 0.065       | 0.353       | 0.005       | 0.004      |
| SM    | 92.3 | 0.065       | 0.353       | 0.005       | 0.004      | 0.75       |
| p (dbar) | 11.9 | 3.06        | 0.56        |            |
| uθ,35 (cm s⁻¹) | 11.6 | 2.73        | 0.55        |            |

Shown are amplitudes of the significant tidal constituents from lunar diurnal K1 to shallow water overides of principal lunar M6. Explained variance through the tidal model in percent is given next to the parameter. Two of the most important tidal constituents are indicated with bold letters. p, pressure; uθ,8, horizontal flow 8 masf; uθ,35, horizontal flow 35 masf; STJS, Stjernsund CWCs; STJp, Stjernsund reference; NL, Nordleksa; GM, Galway Mound; SNC, St. Nazaire Canyon; PE, Pagés Escarpment; VM, Valentine Mound; SM, Sylvester Mound.

- At SM, correlation between uθ,8 and σ0 is moderate (R = 0.62, τ = −1.33 h) meaning that minimum densities are usually reached before the peak mean direction velocities. At these sites the maximum density change within one tidal cycle (M2) (Figure 7B), corresponds to a vertical isopycnal movement of > 120 m at SNC and SM around 80 m at PE and around 2 m at STJp when compared to water column density values (Figure 6).

Hydrodynamics

When local topography, water column structure and velocity measurements are combined, we get flow type estimations for each site. In Figure 9 the results are shown for the time-averaged horizontal velocity (Umean) and peak horizontal velocity (Umax) linked to high tide. The velocities needed for partially blocked flow vary between Ucr = 0.3−80 cm s⁻¹ with time scales tcr = 0.04−6.5 h. At SNC and PE flow is blocked and partially blocked conditions are never met since Ucr is over twice as large as Umax. At GM partially blocked flow is seen once a day (Ucr = 26 cm s⁻¹) except for 7.5.2004. At NL and STJS the flow is partially blocked almost all the time, with Ucr < 3.5 cm s⁻¹. At SM and STJp flow is mostly subcritical, but reaches partially blocked conditions irregularly (0−2 times per day) throughout the study periods. At VM flow is partially blocked twice a day before 20.1.2016 (Ucr = 19.4 cm s⁻¹). After this, the flow speed decreases and flow is subcritical at the site.

Even though the flow is at least partly partially blocked at most of the sites, the formation of hydraulic jump is restricted if the flow is not quasi-steady. This is the case at SM, where advection time scale is larger than the buoyancy period (ε = 2.8).
Table 5 | Cross-correlations between mean direction velocity component at 8 m asf ($U_{m,8}$) with sigma-theta ($\sigma_8$), vertical velocity component at 8 m asf ($u_{w,8}$) and the mean direction velocity component at 35 m asf ($U_{m,35}$) with maximum correlation ($R$) and offset ($\tau$) in hours.

| Sites       | $U_{m,8}$ | $U_{m,8}$ | $U_{m,8}$ |
|-------------|-----------|-----------|-----------|
|             | $\sigma_8$ | $u_{w,8}$ | $U_{m,35}$ |
| STJs        | 0.92      | -0.3      | 0.97      |
| STJp        | 0.18      | -2.17     | 0.73      |
| NL          | -0.66     | 4.88      | 0.89      |
| GM          | -0.87     | 5.67      | 0.92      |
| SNC         | -0.24     | 0.5       | 0.16      |
| PE          | -0.29     | -8.83     | -0.44     |
| SM          | 0.75      | -2.67     | 0.61      |
| SM          | 0.62      | -1.33     | 0.37      |

STJs, Stjømnund CWCs; STJp, Stjømnund reference; NL, Nordekkisa; GM, Galway Mound; SNC, St. Nazaire Canyon; PE, Pagès Escarpment; VM, Valentine Mound; SM, Sylvester Mound.

The isopycnal displacement ($\Delta h = U_{mean}/N$) is $>60$ m at STJs and GM, between 15–25 m at NL, VM and SM, around 11 m at PE and STJp and 6 m at SNC. This is restricted by layer thickness ratio at NL ($r > 0.5$) and the height of the morphologic structure at SM ($U_{mean}/N > b_{m}$).

When the tide turns, flow relaxes and the upstream wave can propagate upward as a non-linear internal bore if the formation of the hydraulic jump has been under hydrostatic conditions. Strong mean volume backscatter signals (Sv) coincide with this relaxation phase at GM (Figure 8). The signal of resuspended particles propagates upward $\sim$10 m h$^{-1}$ over 6 h and the signal of the settling particles is visible for the next 12 h. Weaker and distorted semi-diurnal signals are seen at NL, STJs and VM (not shown). At SM and at STJp the fluctuation of the strong Sv signals are neither diurnal nor semi-diurnal but irregular with some stronger signals during the study period. At SNC and at PE there is no structure in Sv.

**DISCUSSION**

At reef scales, several parameters coincide with healthy and high quality CWC occurrences: relatively anisotropic flow with oscillating flow direction, hydrostatic partially blocked flow during high tide, and strong correlation between velocity parameters and bottom density. These can be shown with the Froude number (Fr)–topography height ratio (Hm) diagram (Baines and Johnson, 2016). Healthy CWCs are found at sites, where regular hydraulic control of tidal flow leads to enhanced hydraulic jumps, local overturning, and internal bores. These processes provide several food-supply sources and prevent sedimentation.

This process has previously been reported as the major driver for oscillation of water mass interface and vertical mixing at CWC reefs. The linked overturning is assumed to carry deep water and re-suspended particles to the CWCs (Davies et al., 2009). The turn of the tide is linked to enhanced mixing, overturning, and increasing oxygen levels at CWC depths (Davies et al., 2009; Soetaert et al., 2016). Model studies suggest that downward movement can be very fast, transporting particles from the surface to intermediate depths ($>500$ m) in less than an hour (Soetaert et al., 2016). Based on observations, the strength of the overturning is linked to the height of the CWC mounds (Cyr et al., 2016). In simulations, the overturning strength is enhanced by steep topographic slopes (large $b_{m}/L$) and slowly oscillating flows (large $\omega$ and vertical tidal excursion) (Legg and Klymak, 2008). Decreasing stratification leads to larger vertical length scales of overturning, as the vertical displacement scale ($\Delta h = U/N$) increases (Legg and Klymak, 2008). Our observations strengthen the theory that hydraulic control of tidal flow is important to CWC growth on basin scales. The strength of the process varies with the health status of the sites.

**State of Flow as a CWC Reef Growth Indicator**

Our results indicate that living and healthy CWCs concentrate at sites, where quasi-steady tidal flow is partially blocked. To compare our results to literature data, we add data from five Atlantic CWC sites. These include three category I sites from offshore Ireland [SE Rockall Bank: Haas CWC mound (hm), an unnamed smaller mound (um) (Cyr et al., 2016) and the Mingulay Reef complex (mrc) (Davies et al., 2009)]. One category II site from the Gulf of Mexico (Campeche CWC mound (cm)) (Hebbeln et al., 2014) and one category IV site from the Gulf of Cadiz (Pen Duick Escarpment, pde) (Mienis et al., 2012) are also used. Their calculated hydrodynamical parameters are described in Table 6 and their state of flow in Figure 9.

With a total of 12 sites and 13 locations, we can distinguish four different cases linking Fr–Hm to CWC growth. These are healthy category I CWC mounds (GM and hm) with regularly partially blocked flow with $H_m > 1.5$ (state PB$_j$), healthy category I CWC sites (STJs, NL, um and mrc) with partially blocked flow with $H_m ≈ 1$ (state PB), category II and IV CWC sites (SM, cm and VM) and non-coral subsite (STJp) with partially subcritical flow with $H_m < 0.6$ (state PB$_s$), dead or declining sites in category III–IV (SNC, PE and pde) with constantly blocked flow (state B) with partially subcritical flow.

At healthy CWC mounds with regularly partially blocked flow (PB$_j$), the flow is partially blocked only when flow speeds are higher than the mean flow ($U_{cr} > U_{mean}$). It seems that the higher the speed required for the partially blocked situation, the stronger the hydraulic jump and generation of internal bores. At hm ($U_{cr} = 46$ cm s$^{-1}$ and $U_{max} = 50$ cm s$^{-1}$) overturning with over 100 m isopycnal displacement is reported only during spring tides (Cyr et al., 2016) and at GM ($U_{cr} = 26$ cm s$^{-1}$ and $U_{max} = 61$ cm s$^{-1}$) the estimated maximum isopycnal displacement is over 70 m (see Section “Hydrodynamics”). Both GM and hm are tall (>100 m) CWC mounds where corals have been growing without hiatus since the last glacial (Eisele et al., 2008; Mienis et al., 2009) and where corals are virtually absent from the summit. This strengthens the idea first given by Cyr et al. (2016), that CWC mounds can reach a maximum height favorable for turbulent
environments under present hydrodynamical conditions. This height is the limit, because mound starts to block the flow during neap tide, preventing the mixing to reach its summit regularly and the mound reaches a steady state where it no longer grows vertically.

Healthy CWC sites with $H_m \approx 1$ (PB) have partially blocked flow conditions even under very low velocities. This creates a turbulent environment over the topographic feature. The site morphologies vary from small ($b_m < 100$ m) CWC mounds (um and mrc) to sill and bank settings (NL and STJ$_S$). At all sites, corals have been growing since the last glacial period (López Correa et al., 2012; Douarin et al., 2014). At NL, um and mrc corals grow on the summit of the mounds and bank. At STJ$_S$ corals do not grow at the summit but on the flanks of the sill.

Partially subcritical sites (PB$_{sc}$) have subcritical conditions during mean or low horizontal velocities and partially blocked conditions during the peak velocity phase. VM and cm are both healthy (category II) CWC sites, where corals have been growing continuously for at least 34 ka (Wefing et al., 2017) and 10.1 ka (Matos et al., 2017), respectively. Even though flow at SM is partially blocked, corals have vanished there around 5 ka ago. This time coincides with the intensification in upwelling and a decline in oxygen (Tamborrino et al., 2019) within the area. The reference site (STJ$_P$) is located in a portion of the sound with a horizontal sea-floor and with low flow velocity. Even though the hydrographical (temperature, salinity, oxygen) ranges are suitable for CWC growth, there is no local overturning or mixing that would enhance particle flow to this point. Both SM and STJ$_P$ have unsteady flow over the tidal cycle and no hydraulic jumps are expected during the partially blocked flow conditions.

Dead or declining sites (B) are found in the Bay of Biscay and the Gulf of Cadiz, where corals are reported to live at the edge of their survival limit and most of the CWC findings are from dead sites. In the Gulf of Cadiz, large scale coral growth has stopped around 9 ka ago (Wienberg et al., 2010). Common for these sites are low flow velocities ($U_{max} < 25$ cm s$^{-1}$) and high sedimentation rates which cause corals to be covered with sediments (Mienis et al., 2012). Since the flow is always blocked, there are no mixing processes over topography. Particles in the water column are evenly distributed most likely due to slow currents and low tidal activity (Bernárdez et al., 2017). This might be the reason, why there is no structure in the backscatter signal at SNC and PE. Even when the favorable hydrographical conditions are met, hydrodynamics prevents veritable coral frameworks to grow on these sites.

Besides the partially blocked flow state, the flow has to be quasi-steady and topography tall compared to isopycnal movement so that flow disturbances have time to grow and develop. The PB$_B$ sites have quasi-steady flow and the topography height does not limit the maximum vertical displacement, $\Delta h$. For PB sites the flow is quasi-steady over the tidal cycle, but the water layer ratio ($r > 0.5$) at NL and mrc affects the vertical displacement of the isopycnals. The flow is not quasi-steady at totally blocked sites (B) at Bay of Biscay, since the time scale is too short ($Ex \approx 1$) and the sites act as internal wave maker. At pde, the flow is quasi-steady, but totally blocked. For the
**FIGURE 9** | The two-layer Froude number, topography height ratio (Fr, H\_m) diagram. Mean horizontal flow velocity (square) and maximum horizontal flow velocity (circle) cases are shown. Sites used in this study (STJ\_S, Stjernsund CWCs; STJ\_P, Stjernsund reference; NL, Nordleksa; GM, Galway Mound; SNC, St. Nazaire Canyon; PE, Pagès Escarpment; VM, Valentine Mounds; SM, Sylvester Mound) are shown in capital letters. Sites from literature (hm, Haas CWC mound; um, unnamed smaller mound; mrc, Mingulay Reef complex; cm, Campeche CWC mound; pde, Pen Duick Escarpment) are written with small letters. CWC categories marked in colors (blue: I, green: II, orange: III, red: IV and CWC absence). The four CWC growth states are shown with ellipses; PB\_bc: Healthy category II sites with mostly completely blocked flow where partially blocked flow conditions are met only during the high or spring tide, B: Dead or declining sites in category III–IV with constantly blocked flow. The locations SM and STJ\_P are excluded from the growth states since the flow is not quasi-steady during the high tide. Flow type separation lines after (Baines, 1998).

**TABLE 6** | Dynamical deep sea parameters for CWC sites and the parameters to estimate the quasi-steady flow conditions.

| Site | Cat | (Fr\_H\_m) | Fr\_0 | Fr\_inert | Fr\_topo | Fr\_Zw\^-1 | \(\Delta h\) (m) | r | \(\varepsilon\) | Ex | Site references |
|------|-----|-----------|------|-----------|----------|-----------|----------------|---|------------|----|----------------|
| GM   | I   | PB\_b     | 0.08 | 0.89      | 0.49     | 1.85      | 78.5           | 0.11 | 0.065       | 4.3 | This study    |
| hm   | I   | PB\_b     | 0.06 | 0.70      | 0.16     | 5.25      | 50.0           | 0.22 | 0.250       | 7.1 | Cyr et al., 2016 |
| STJ\_S | I | PB       | 0.17 | 1.53      | 0.38     | 3.95      | 60.7           | 0.44 | 0.031       | 2.5 | This study    |
| NL   | I   | PB       | 0.08 | 0.88      | 0.14     | 5.80      | 23.8           | 0.6  | 0.003       | 2.9 | This study    |
| um   | I   | PB       | 0.05 | 0.40      | 0.67     | 1.61      | 50.0           | 0.23 | 0.191       | 6.2 | Cyr et al., 2016 |
| mrc  | I   | PB       | 0.33 | 1.08      | 0.89     | 7.22      | 65.2           | 0.63 | 0.199       | 14.5| Davies et al., 2009 |
| VM   | II  | PB\_sc   | 0.03 | 0.22      | 0.19     | 5.75      | 16.7           | 0.35 | 0.027       | 6.1 | This study    |
| cm   | II  | PB\_sc   | 0.09 | 0.30      | 1.61     | 6.40      | 48.4           | 0.06 | 0.294       | 23.8| Hebbeln et al., 2014 |
| SNC  | III | B        | 0.01 | 0.06      | 0.03     | 2.15      | 6.4            | 0.15 | 0.002       | 0.8 | This study    |
| SM   | IV  | PB\_sc   | 0.08 | 0.53      | 1.79     | 9.64      | 17.9           | 0.19 | 2.632       | 66.8| This study    |
| PE   | IV  | B        | 0.01 | 0.08      | 0.03     | 6.02      | 11.3           | 0.16 | 0.004       | 1.0 | This study    |
| pde  | IV  | B        | 0.07 | 0.28      | 0.43     | 3.51      | 44.0           | 0.63 | 0.250       | 7.1 | Menis et al., 2012 |
| STJ\_P | Ref. | PB\_sc | 0.03 | 0.27      | 0.07     | 3.76      | 11.2           | 0.47 | 0.001       | 1.0 | This study    |

Shown are after the name of the sites and CWC categories the flow state (Fr\_H\_m), Froude number for one layer flow (Fr\_0), the internal Froude number, Fr\_inert (Davies et al., 2009), topographical Froude number, Fr\_topo (Cyr et al., 2016), tidal excursion inverse Froude number, Fr\_Zw\^-1 (Legg and Klymak, 2008; Mohn et al., 2014), vertical isopycnal displacement scale, \(\Delta h\) (in meters), the layer thickness ratio, r, non-hydrostatic parameter, \(\varepsilon\), and excursion number, Ex. For details see Sections "Other Representations for Hydraulic Control" and "Data Analysis." GM, Galway Mound; hm, Haas CWC mound; STJ\_P, Stjernsund CWCs; NL, Nordleksa; um, unnamed smaller mound; mrc, Mingulay Reef complex; cm, Campeche CWC mound; SNC, St. Nazaire Canyon; SM, Sylvester Mound; PE, Pagès Escarpment; pde, Pen Duick Escarpment; STJ\_S, Stjernsund reference; PB\_bc, mostly blocked flow with regularly partially blocked conditions; PB, partially blocked flow; PB\_sc, mostly subcritical flow with regularly partially blocked conditions; B, completely blocked flow.
sites that are partially subcritical (\(P_{Bc}\)), the situation is more complicated. For these, only cm and VM have quasi-steady flows, where conditions support hydraulic jumps. At SM, the advection timescale is short relative to buoyancy period (\(\varepsilon > 1\)) and the height of the topography is small compared to possible vertical displacement of the isopycnals (\(b_m < U_{\text{mean}}/N\)). At location STI\(p\), the advection time scale is too short for hydraulic control to occur (\(\varepsilon \approx 1\)).

**Short and Long Term Changes in Velocity Field and Hydrography**

The strength of the bottom currents is affected by the respective phase of the tidal cycle, with maximum velocities occurring during the spring tides. A model study by Soetaert et al. (2016) shows that overturning and mixing at CWC mounds are strongest during spring tide and weakest during neap tide. A 1-week study period is not long enough to capture both, neap and spring tides. Thus, higher than measured velocities can be expected to occur at those sites that were studied during neap tide periods (PE, SM, STJ, mrc and cm). From these, sites SM, STJ, mrc and cm reach partially blocked conditions with measured velocities and at PE the required velocity \(U_{\text{cr}} > 10 \times U_{\text{max}}\). It is unlikely that time varying magnitude of \(U\) would change the flow states of the sites on the \(Fr-H_m\) diagram.

More likely the flow states are affected by the changes in the water column structure. This is driven by short-term and seasonal changes in the wind fields that cause changes in local currents and hydrography. Off southwestern Africa, the biannual change in the Angola–Benguela front is due to changes in the wind field. This causes changes in water masses and hence in oxygen levels at SM (Junker et al., 2017). Trade winds are strongest during May–September, when cold, oxygen-rich ESACW dominates the Namibian margin. The flow reverses during October–April when warm, nutrient-rich and oxygen depleted SACW dominates the area. Anoxic conditions have been reported to occur along the Namibian margin in February–May (Junker et al., 2017). Along the Angolan margin, the wind field is more stable (Shannon et al., 1987) and the near-shore seasonal variations are caused by seasonal variations in the Cuanza and Congo river inputs (Kopete et al., 2017). The seasonality of temperature and stratification are strong on the Norwegian coast (Sætre and Løken, 1971; Mork, 1981). The water column mixes and is weakly stratified during the winter storms. Due to the presence of the WMW, water column is strongly stratified during spring and summer months.

**Environmental Conditions**

Hydrographic (temperature and salinity) and oxygen conditions have been documented from most of the known living CWC sites. The known ranges for \(D. \text{ pertusum}\) in PSS-78/EOS-80 for temperature are 4–13.9°C (Roberts et al., 2006; Freiwald et al., 2009; Davies and Guinotte, 2011), salinity 31.7–38.8 psu (Freiwald et al., 2004; Davies et al., 2008), dissolved oxygen 1.0–7.2 ml l\(^{-1}\) (Dodds et al., 2007; Davies et al., 2008, 2010; Ramos et al., 2017), and sigma-theta 27.35–27.6 kg m\(^{-3}\) (in the eastern Atlantic) (Dullo et al., 2008). The conversion errors between PSS-78/EOS-80 and TEO-10 are small at the Atlantic and thus our results are comparable to the known ranges. The recorded temperature (6.12–12.53°C) and salinity (33.8–36.1 g kg\(^{-1}\)) values fit well into these defined ranges. The CWCs grow in less dense waters at NL and at VM compared to the previously defined ranges, but outside the eastern Atlantic thriving CWCs are found outside this range e.g., in the Mediterranean (Flögel et al., 2014b) and in the Gulf of Mexico (Hebbeln et al., 2014). Corals at Nordleksa are within this sigma-theta range during spring months when the influence of AW is strongest (not shown). At the northern Atlantic sites, dissolved oxygen levels (3.7–6.2 ml l\(^{-1}\)) are well within previously reported limits, but the observed concentration of dissolved oxygen on the Angolan and Namibian margins are both hypoxic. At VM, the corals thrive at the lowest reported oxygen levels of 0.46–0.69 ml l\(^{-1}\) (Hanz et al., 2019).

In summary, given the enormous ranges of hydrographic and oxygen conditions a clear link to ideal environmental conditions for CWC growth cannot be drawn and most likely these factors are of secondary importance.

Our study suggests that the local food supply is important part of ideal environmental conditions for CWCs. The thriving coral sites (category I and II) described in this study benefit both hydrodynamical processes that deliver food particles on diurnal bases to corals during maximum flow phases (partially blocked flow conditions with \(U_{\text{max}}\)) and low velocity phases (\(U < 7 \text{ cm s}^{-1}\) for < 40% of the time) for optimal food capture (Purser et al., 2010; Orejas et al., 2016) whereas the declining sites showed unfavorable conditions for hydrodynamical food supply processes (blocked flow conditions, flow speed mostly < 7 cm s\(^{-1}\)). Sufficient level of food is crucial to CWCs since under starvation both coral fitness and physiological performance drop (Naumann et al., 2011; Larsson et al., 2013; Baussant et al., 2017). In elevated temperature conditions, increased food supply has been observed to stimulate CWC growth but not to compensate for adverse effects of ocean acidification (Büscher et al., 2017). Under low pH and undersaturated aragonite conditions, CWC net calcification has been observed to decrease but the high quality food supply mitigates the physiological impacts on respiration and prey capture (Georgian et al., 2016b). In field studies, corals are found to even thrive in hypoxic conditions in the Gulf of Mexico (Lunden et al., 2014; Georgian et al., 2016a) and off Namibia (Hanz et al., 2019) as long as sufficient high quality food is available whereas laboratory studies have shown coral mortality in hypoxic conditions (Dodds et al., 2007; Lunden et al., 2014) and in water temperatures > 14°C (Lunden et al., 2014).
another site (e.g., Frank et al., 2011). During glacial periods the sea level has been about 120 m below the present and hence the tidal interaction level has been deeper than in the modern ocean. The change of the depth of the water mass boundaries on glacial/interglacial time scales has been suggested as an explanation for CWC reef development (Wang et al., 2019). A recent study by Hebbeln et al. (2019) highlights the food supply as the most prominent key driver of demise/re-establishment of the CWCs and stresses the interactions between the water column and the local hydrodynamics. 

Under ongoing global change, the ocean is predicted to become warmer, more acidic and less oxygenated. The discussed studies have shown the negative effects of rising temperature (e.g., Lunden et al., 2014), ocean acidification (Gómez et al., 2018) and ocean deoxygenation (Fink et al., 2012) and their interactions (Büscher et al., 2017; Wienberg et al., 2018) on CWC ecosystems but the projected changes in climate will also shift the primary productivity northeasterswards (Barton et al., 2016) due to changes in ocean warming, circulation and stratification. The latter two will also affect the tidal dynamics control and CWC growth described here more than predicted sea-level rise (few centimeters per decade, Dangendorf et al., 2017) within the next decades when both overall density decreases and the surface stratification (upper 200 m) strengthens (Capotondi et al., 2012). The stratification maxima and hence the layer thicknesses will change depending of the area. If the N maximum moves toward surface, topography height ratio (Hm) will decrease. On the other hand, larger differences in the upper and lower layer densities will yield increase in the speed of the long waves and hence decrease in Froude number (Fr). Together these changes would shift the flow states in Fr-Hm diagram toward the down-left corner and sites which are currently PB or healthy small mounds on subcritical boundary, may not experience partially blocked conditions in future.

Other Representations for Hydraulic Control

Simple one-layer flow in relatively shallow water Fr0 = Umean/(NH) gives only little information from the deep-water coral sites. Therefore, several estimations (Equation 2) have been used to capture the dynamics around the CWCs. In addition to the two-layer Froude number used in this study, these are the internal Froude number, Frinert (Davies et al., 2009), topographical Froude number, Frm (Cyr et al., 2016), and tidal excursion inverse Froude number, Frzw⁻¹ (Legg and Klymak, 2008; Mohn et al., 2014), where,

\[ Fr_{inert} = \frac{U_{max} \pi}{N (H - b_m)} \approx \frac{U_{max} \pi}{\sqrt{g(\rho_s - \rho) (H - b_m)}} \]

\[ Fr_{topo} = \frac{U_{mean}}{Nb_m}, Fr_{zw}^{-1} = \frac{dh N}{dx} \approx \frac{N 2b_m}{\omega L} e^{-0.5} \]  

(2)

Where \( \rho_s \) is water density at summit depth, \( \rho_s \) is the surface water density and \( \rho_{mean} \) is the mean density of the water column. From these, quasi-steady conditions (Ex > 1 and \( c < 1 \)) are expected when using Frinert and Frtopo. The Frzw⁻¹ is independent from the magnitude of the flow. The values for these dynamical parameters are shown in Table 6.

Frinert describes the flow conditions over the crest depth of the morphologic structures. Similar to Fr0, hydraulic control is expected when Frinert ≈ 1. This parameter picks well the sites with known overturning since Frinert = 1 ± 0.2 at GM, hm, mrc and NL. For the two category I not in this range, the flow is supercritical at STJ (Frinert = 1.53) and subcritical at um (Frinert = 0.4). For other sites, the flow with Frinert is subcritical (< 0.53).

Frtopo describes the obstruction of the steady flow by the topography (Legg and Klymak, 2008). The values Frtopo ≪ 1 are used to describe conditions where overturning is possible. For conditions with small Frtopo, however, the disturbances will be restricted to the horizontal plane. As Frtopo increases toward 1, non-linear lee-waves are expected to occur. The range for this non-linear regime is suggested to be Frtopo = 0.5–0.8 (Baines, 1998; Vosper et al., 1999). At large Frtopo, the flow may exhibit three-dimensional wakes and be more turbulent (Dewey et al., 2005). Of sites used in this study, Frtopo > 1 at VM and cm. Within the 0.5–0.8 range are GM and um. Mingulay reef complex (Frtopo = 0.89) and Haas mound (Frtopo = 0.16) are known for overturning events, but with the values used, this is not shown with this estimation.

The tidal excursion inverse Froude number describes the effect of vertical tidal excursion distance and stratification over a tidal cycle to bottom flow. Internal jumps are expected in high velocity and weak stratification regimes with Frzw⁻¹ > 3. The hydrodynamic model study from NE Atlantic by Mohn et al. (2014) shows that areas with coral present have higher Frzw⁻¹ values than coral absence and background areas (Frzw⁻¹ < 1.5). All of the sites used in this study have Frzw⁻¹ > 1.5. Surprisingly, GM, um and SNC are the only sites with Frzw⁻¹ < 3.

These parameters describing the bottom flow dynamics depend on local water column characteristics such as stratification and depth, the dimensions of the topographic feature and the bottom flow. It is important that the right parameter is used for further model studies and hydraulic control estimations driven from observations.

CONCLUSION

The data of this study represent a compilation of stratification, ambient water mass characteristics and the bottom water flow at CWC sites colonized by D. pertusum in the eastern Atlantic from the Arctic to the southern hemisphere. It sheds new light on the processes which determine coral distribution and growth. Even though large scale environmental conditions are useful for statistical habitat suitability models, on the reef scale hydrodynamical processes give more information about the quality of the coral occurrences. High-quality and healthy D. pertusum reefs are found in areas where quasi-steady tidal
flow is partially blocked by the CWC morphology and the two-layer Froude number is $> 0.35$ and the topography height ratio $H_m = 0.3–1.7$. Our study suggests that the hydrodynamical setting causes a quasi-steady particle supply for filter-feeding corals. In contrast to episodic food supply theories based on spring blooms, our observations suggest diurnal re-supply of sinking particles back to the water column to heights that are in reach for the feeding the CWCs. Steady (diurnal basis) supply of high-quality food would be a key factor when diagnosing a change in the CWC environment, where environmental stress set by e.g., ocean acidification (low pH) or low oxygen concentrations, may be of secondary importance but will increase food and energy demand. Indeed, the local stratification (e.g., the vertical displacement of the isopycnals) and the topography are important factors that determine the strength of the internal tidal bores and thus keep the particles resupply process running. Changes in stratification, flow magnitude and the height of the morphologic structure (e.g., by sea level changes during glacial/non-glacial periods, by ocean warming/cooling or by outgrowth of the CWC mounds) may cause starving of the CWC habitat. The future plan is to link hydraulic control to vertical growth rates as well as to distinguish the different food sources by estimating the uptake of resuspended particles.

**DATA AVAILABILITY STATEMENT**

The datasets generated for this study are available on request to the corresponding author. The cruise M122 CTD data is available: https://doi.pangaea.de/10.1594/PANGAEA.904192.

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**AUTHOR CONTRIBUTIONS**

SF led the project. KJ performed the analyses and interpretation of the results with assistance from JK. KJ wrote the manuscript with assistance from SF. All authors contributed substantially to the work and revision of the manuscript.

**FUNDING**

This study was supported by several agencies and projects: Helmholtz association funded projects HGF ROBEX, HGF ARCHES, HGF ACROSS, and HGF MOSES. Also project BMBF MOLAB and European Union’s Horizon 2020 Research and Innovation Program under grant agreement 63321 (AtlantOS). Supported the cruises and data collection and the GEOMAR Helmholtz Centre for Ocean Research Kiel provided the facilities to conduct the study. KJ was funded by the Research Council of Norway project Fate of cold-water coral reefs – identifying drivers of ecosystem change (FATE) and by the Osk. Huttunen Foundation doctorate researcher grant.

**ACKNOWLEDGMENTS**

We would like to thank captains, crew, chief-scientists, and scientific teams during cruises M122, POS473, POS455, POS438, POS434, M84-5, POS325, POS16, and M61 on RV Meteor and on RV Poseidon (2004–2016). We are also grateful for the valuable feedback provided by the two reviewers, Marina Carreiro-Silva and Lorenzo Angeletti.
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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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