Cold-water coral framework architecture is selectively shaped by bottom current flow

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Abstract   The three-dimensional (3D) structure of habitat-forming corals has profound impacts on reef ecosystem processes. Elucidating coral structural responses to the environment is therefore crucial to understand changes in these ecosystems. However, little is known of how environmental factors shape coral structure in deep and dark waters, where cold-water coral (CWC) reefs thrive. Here, we attempt to infer the influence of current flow on CWC framework architecture, using 3D scanning to quantify colony shape traits (volume compactness and surface complexity) in the reef-building CWC *Desmophyllum pertusum* from adjacent fjord and offshore habitats with contrasting flow regimes. We find substantial architectural variability both between and within habitats. We show that corals are generally more compact in the fjord habitat, reflecting the prevailing higher current speeds, although differences in volume compactness between fjord and offshore corals are more subtle when comparing the fjord with the more exposed side of the offshore setting, probably due to locally intensified currents. Conversely, we observe no clear disparity in coral surface complexity between habitats (despite its positive correlation with volume compactness), suggesting it is not affected by current speed. Unlike volume compactness, surface complexity is similarly variable within a single colony as it is between colonies within the same habitat or between habitats and is therefore perhaps more dependent than volume compactness on microenvironmental conditions. These findings suggest a highly plastic, trait-specific and functionally relevant structural response of CWCs to current flow and underscore the importance of multiple concurrent sources of hydrodynamic forcing on CWC growth.

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Introduction

Cold-water coral (CWC) reefs are biodiversity-rich ecosystems found in a vast range of water depths and habitats, down to over 1000 m of depth on seamounts and continental slopes (Freiwald et al. 2004), and up to 39 m in Norwegian fjords (Fosså et al. 2002). These ecosystems rely on the three-dimensional (3D) skeletal frameworks formed by a few species of azooxanthellate scleractinians such as the widely distributed *Desmophyllum pertusum* (previously known as *Lophelia pertusa*), the primary framework builder in the North Atlantic Ocean (Freiwald et al. 2004). The majority of the CWC reef framework consists of dead coral skeleton (devoid of living tissue) (Vad et al. 2017), which supports key ecological functions modulated by its physical branching structure, including habitat provision for most of the

numerous reef-associated species (Mortensen et al. 1995) and baffling and retention of suspended sediment and particulate organic matter (Wheeler et al. 2005; Maier et al. 2021; Wang et al. 2021). Skeletal traits of reef-building corals are indeed known to broadly affect not only their individual performance and response to the environment, but also ecosystem processes, i.e. they represent both response and effect traits (Suding et al. 2008; Zawada et al. 2019b). For example, branch spacing in shallow-water *Acropora* spp. varies in response to light and water motion (Bottjer 1980; Oliver et al. 1983; Kaniewska et al. 2008), influencing in turn abundance and size of associated epifauna (Vytopil and Willis 2001), and can therefore be used to evaluate the impact of disturbance and environmental change on reef functional diversity (e.g. McWilliam et al. 2020). Skeletal traits assume particular significance in a CWC reef, as this is typically constructed by only one or two species at a given location (Freiwald 2002). Hence, knowing how CWC skeletal morphology is controlled by environmental variation is vital to better understand benthic ecosystem functioning in response to future change.

Light and water motion (especially wave stress), as exemplified above, are generally regarded as the most important environmental drivers of shallow-water coral morphology (Todd 2008). Here, we focus only on water motion, because CWCs inhabit deep aphotic waters and lack symbiotic zooxanthellae. In shallow-water corals, water movement is known to prevent sediment smothering, enhance nutrient availability and diffusion (Todd 2008) and favour waste removal (Chamberlain and Graus 1975), but also to cause mechanical stress on their rigid skeletal structure (Graus et al. 1977). A typical response of shallow-water branching corals to increased water motion consists of acquiring a more compact architecture with shorter, thicker and/or more crowded branches (e.g. Veron and Pichon 1976; Bottjer 1980), which grants higher mechanical resistance to flow-induced breakage (Graus et al. 1977) and, by slowing down currents more effectively (Chamberlain and Graus 1975), allows efficient food capture (Sebens et al. 1997). Phenotypic responses of this kind result from plasticity and/or adaptation (Todd 2008) and vary across multiple spatial levels, from within colonies to between geographic regions (Veron 1982).

It is unclear whether water motion affects coral skeletal morphology analogously in deep waters, where light levels and storm wave damage do not play a role but currents have even greater physiological relevance, given that CWCs primarily feed on suspended food sources (e.g. zooplankton and particulate organic matter; Mueller et al. 2014). Computational modelling has recently started to elucidate the fine-scale interactions between flow velocity and CWC growth, highlighting their complex interplay mediated by coral feeding efficiency and energetic reserves (Hennige et al. 2021). Although *D. pertusum* does seem to follow

similar morphological trends to shallow-water species in response to current intensity (De Clippele et al. 2018; Büscher et al. 2019; Sanna and Freiwald 2021), the available evidence is mostly qualitative (e.g. based on discrete morphological categorisations) and very little is known about the mechanisms, magnitude and scales of this presumed hydrodynamic control. The logistic difficulties of working in the deep ocean and the relatively slow growth of CWC colonies (Lartaud et al. 2017) have thus far hampered adequate investigation (either in situ or in aquarium) of their morphological responses to environmental factors. Photogrammetry based on remotely operated vehicle (ROV) video data is an increasingly common methodology for the detailed characterisation of 3D structure and ecology of CWC reef habitats (Price et al. 2019; Lim et al. 2020), but its resolution is still insufficient to capture the fine-scale morphology of CWC colonies. Here, we investigate how CWCs are shaped by habitat-specific and local topography-induced flow regimes, by quantifying the skeletal architecture of physical colony samples of *D. pertusum* from mid-Norwegian inshore (fjord) and offshore shelf habitats with high-resolution 3D scanning. The hydro-physicochemical affinity of these adjacent habitats provides the rare opportunity to elucidate the long-term effects of hydrodynamic forcing on CWC framework architecture while ruling out other environmental effects as much as possible.

Materials and methods

Study areas

We used a natural experiment involving two postglacial *Desmophyllum pertusum* reef sites which occur in close proximity, but distinct habitats across the mid-Norwegian continental shelf: the inshore, shallower Nordleksa Reef, and the offshore Sula Reef Complex (Fig. 1). Another mid-Norwegian offshore site, Træna, was included in the study to account for the intracolonial variation of *D. pertusum*, given the availability of several co-occurring samples from this location.

The Nordleksa Reef is found at water depths between 145 and 210 m near the island of Nordleksa, at the entrance of the Trondheim Fjord, extending over a length of ~ 1.7 km from west to east with two main reef summits (Juva et al. 2020). The Sula Reef Complex is made up of numerous individual reefs (isolated or coalescent) up to 35 m high, occurring at 240–315 m depth over a distance of ~ 14 km on the Sula Ridge, a narrow southwest–northeast-trending asymmetrical spur with a steep escarpment along the southeast side (Freiwald et al. 2002; Fig. 1b). Large-scale circulation over the Nordleksa Reef and the Sula Reef Complex is dominated by the Norwegian Coastal Current and the
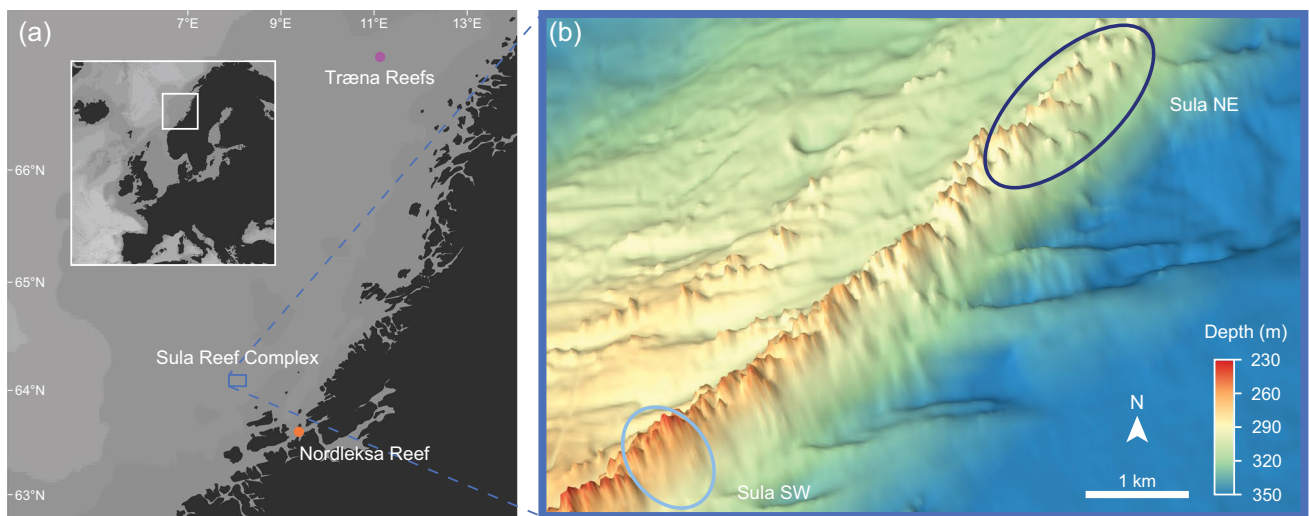
Fig. 1 Study areas. **a** Location of the reef study sites in mid-Norwegian waters. **b** 3D bathymetric map of the Sula Reef Complex (10× vertical exaggeration), with study areas delimited by ellipses.

Map based on 5×5 m grid bathymetry data by MAREANO (Buhl-Mortensen et al. 2015; ©Kartverket)

underlying, denser North Atlantic Current, both flowing northwards along the Norwegian margin (Freiwald et al. 2002). In another study still to be published, water mass characteristics and hydrodynamics were investigated at Nordleksa (63° 36.45′ N, 09° 22.92′ E at 217 m depth) and Sula (64° 06.66′ N, 08° 07.12′ E at 305 m depth) over one year (summer 2013–2014) by benthic landers. Variations in horizontal flow speed and direction during this period are shown in Fig. 2. Despite their proximity, the flow regimes of these two sites differ markedly: at Nordleksa, bottom currents are under strong tidal control (tidal fluctuations explained ca. 60% of their horizontal velocities) and showed higher mean annual horizontal speed (~ 18 cm s^{-1}) compared to Sula (~ 8 cm s^{-1}) (Fig. 2; Büscher et al. in prep.). Nonetheless, instantaneous horizontal flow velocities can be far higher and reached peak speeds of 104 cm s^{-1} at Nordleksa and 157 cm s^{-1} at Sula (Büscher et al. in prep.). At Nordleksa, partially blocked flow conditions promote turbulence (Juva
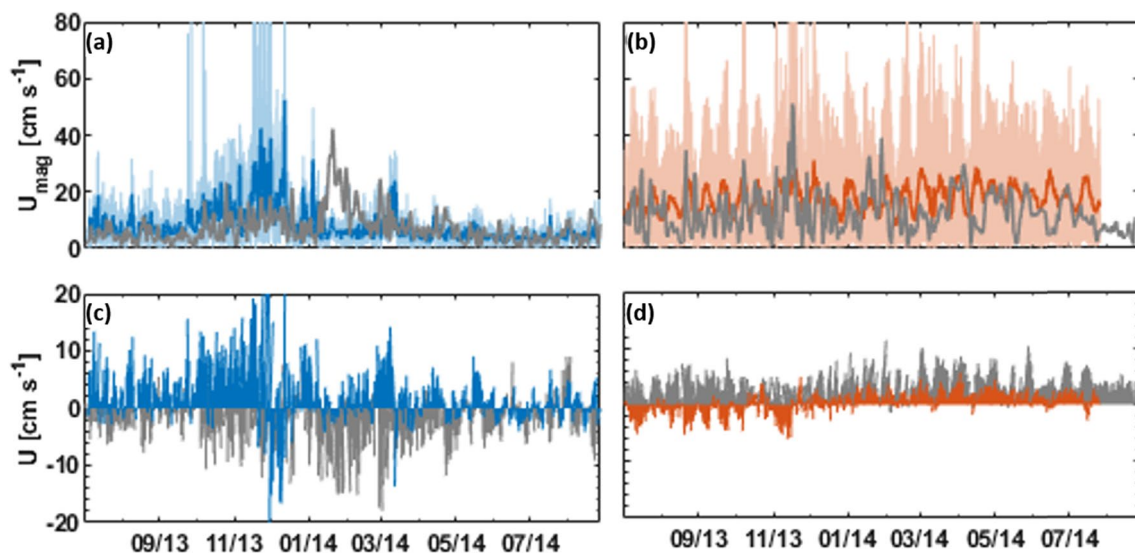

Fig. 2 Bottom flow speed (U$_{mag}$) (**a**, **b**) and average flow speed in north–south horizontal flow direction (**c**, **d**; up = north, down = south), measured over one year by benthic landers at Sula (left panels, **a**+**c**, blue) and Nordleksa (right panels, **b**+**d**, orange).

The thicker lines in **a** and **b** show the 1-day running mean, and the horizontal direction in **c** and **d** is shown with 1-day resolution. The flow data are compared with NorKyst-800-model data (grey) (Albretsen et al. 2011) for the respective sites

et al. 2020). While flow velocity and direction can vary significantly and rather instantaneously (due to e.g. interaction with complex local topography), other hydrographic parameters vary on smaller scales and more gradually, allowing us to constrain the impact of bottom currents. During the benthic deployment period between 2013 and 2014, the mean annual bottom temperature was slightly warmer at Nordleksa with 7.9 ± 0.3 °C compared to 7.5 ± 0.3 °C at Sula, while mean annual bottom salinity was lower at Nordleksa (34.8 ± 0.2 g kg^{-1} absolute salinity) compared to Sula (35.1 ± 0.5 g kg^{-1} absolute salinity) (Büscher et al. in prep.). The pH as measured by distinct water samples collected close to live corals at both sites was 7.99–8.05 at Nordleksa (depending on depth and proximity to corals) and 8.04 at Sula (Büscher et al. 2019).

To appraise the role of flow regimes driven by local seafloor topography, we selected two distinct areas on opposite sides of Sula Ridge's long axis, separated by approximately 5 km, one area in the southwest part of the ridge (henceforth, Sula SW) and the other in the northeast part (Sula NE) (Fig. 1b). Sula SW is characterised by higher relief and a steeper ridge escarpment (Thorsnes et al. 2015), which presumably expose the corals to stronger bottom currents due to topographic acceleration of flow (Thorsnes et al. 2016).

The Træna site consists of elongated reefs found at 300–330 m depth in the Træna Deep (Wehrmann et al. 2009), a trough located north of Nordleksa and Sula (Fig. 1a).

Study material

We focused on the dead skeletal framework of *D. pertusum* because, in addition to its high ecological significance, it represents a mature colony stage that was exposed to the surrounding environmental conditions throughout its development (unlike still-growing live colony layers). Since sampling entire colonies (capable of reaching a diameter of a couple of metres) from the seabed is logistically and ecologically problematic, we used a collection of dead coral blocks retaining a unitary 3D structure, fist-sized or larger (up to ~30 cm in height) and comprising at least 30 corallites (i.e. the skeletal cups of individual polyps), so as to be representative of the 3D coral framework (Fig. 3a). When fragmentation appeared to have altered the original framework structure (e.g. forming large concavities), we either discarded the specimen or, whenever possible, further fragmented it into a unitary piece of suitable size by removing peripheral isolated branches. Samples were also cleaned from sediment and large epizoans (e.g. sponges, bivalves) using a brush and tweezers, to prevent inaccurate representation of the skeletal surface.

Low statistical sample sizes are usually unavoidable when working with large CWC fragments. Our study represents
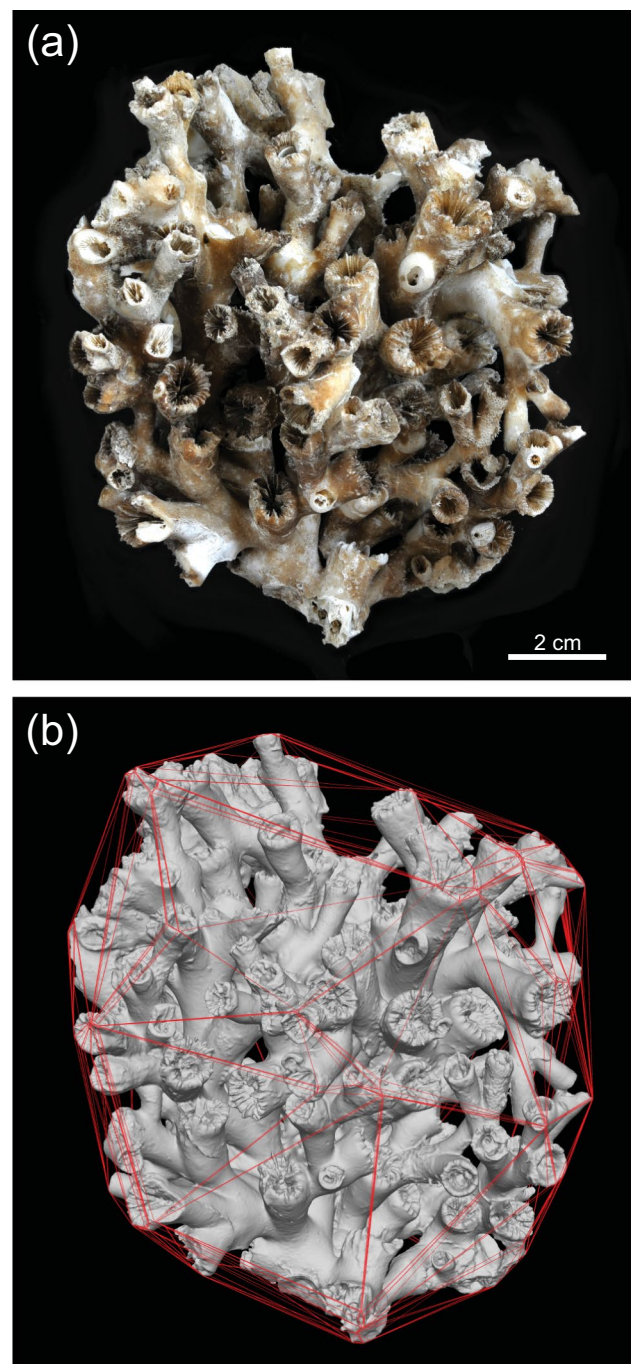
Fig. 3 a Exemplary *Desmophyllum pertusum* colony sample (SaM 42879) and **b** its 3D reconstruction, with wireframe representation (showing only geometric edges) of the convex hull in red

a convenient exception in this sense (see also Büscher et al. 2019), as we managed to incorporate a relatively high number of suitable samples ($n = 58$; Supplementary Information, Table S1), collected by research cruises during repeated surveys of the study areas over a time span of 20 years (1994–2013). At Nordleksa and Sula, samples had been collected across the reefs mostly with mobile gear (dredge

and submersible), considerably reducing the probability of sampling the same colony multiple times. Another indication of their origin from different colonies was their wide variety of preservation states. Conversely, Træna samples had all been collected from the same spot on a reef top with a single box core ($50 \times 50 \times 60$ cm), and hence, they were most likely part of the same colony, with negligible bathymetric variation. All samples showed the typical extra-calcification induced by the symbiotic polychaete worm *Eunice norvegica* (Freiwald and Wilson 1998), albeit to varying extents.

3D shape quantification

Digital 3D surface models of the coral samples were produced using the structured-light 3D scanner Artec Space Spider with the software Artec Studio 15 (Artec 3D, Luxembourg). Since 3D surface scanning only captures the external morphology of objects, artefacts might develop when working with densely branched specimens, due to self-shading (Reichert et al. 2016). To minimise this effect, we performed several individual scans of each specimen with different orientations. Noise was removed from individual scans with the *Eraser* tool. Watertight triangle meshes with a resolution of 0.2 mm (Fig. 3b) were created via the *Sharp fusion* algorithm, and, when necessary, further cleaned from artefacts using the *Small-object filter*, *Eraser* and *Defeature brush* tools. Another consequence of surface-based scanning was that corallites, as well as encrusted *E. norvegica* tubes, despite being at least partially hollow, were generally modelled as completely solid elements, which may not reflect the actual mechanical properties of colonies. However, this is not problematic within the scope of our study, as we focused on how the CWC skeleton is spatially distributed in the environment.

We characterised coral architecture on the basis of two morphological traits of high functional relevance, volume compactness and surface complexity, related to fundamental geometric properties (volume and surface area) and both affecting habitat provision for reef-associated organisms. Moreover, volume compactness is particularly indicative of structural robustness and interstitial space available for sediment accumulation, whereas surface complexity is more closely linked to the density of living tissue biomass (Zawada et al. 2019a, b). To quantify these traits, we calculated for each digital model two 3D shape variables, *compactness* and *packing*, representing volume compactness and surface complexity, respectively. *Compactness* measures how different parts of an object fill the space surrounding it and is the ratio of object volume to the volume of its convex hull (Merks et al. 2003), with the convex hull being the smallest convex region that encloses the object. The same variable is called *proportion occupied* in Doszpot et al. (2019) and *convexity* in Zawada et al. (2019a, b).

Packing measures how the surface area of an object is packed within the object bulk and is the ratio of object surface area to convex hull surface area (Zawada et al. 2019b); it was shown to be strongly correlated with *fractal dimension* (Zawada et al. 2019a), another important metric of coral complexity (Reichert et al. 2017). Such dimensionless shape variables are independent of size and orientation, unlike other metrics of coral morphology like ratio of surface area to volume (Doszpot et al. 2019) and first moments of volume and surface area (Zawada et al. 2019a). This allowed us to focus exclusively on shape and makes the two variables particularly suitable for our samples, consisting of colony portions of various sizes, rather than whole colonies. Both variables were obtained from volume and surface area measures of the 3D meshes and respective convex hulls (Fig. 3b), computed in MeshLab v2020.12 (Cignoni et al. 2008).

Statistical analysis

We evaluated the association between CWC volume compactness (described by *compactness*) and surface complexity (described by *packing*) using Spearman's rank correlation (as *compactness* had a non-normal distribution). To comparatively assess the effects of habitat-specific and local topography-induced flow regimes on CWC architecture, differences between Nordleksa, Sula SW and Sula NE were tested using one-way ANOVA with Tukey's post hoc test and Cohen's *d* effect size (calculated with the R package *effsize*;
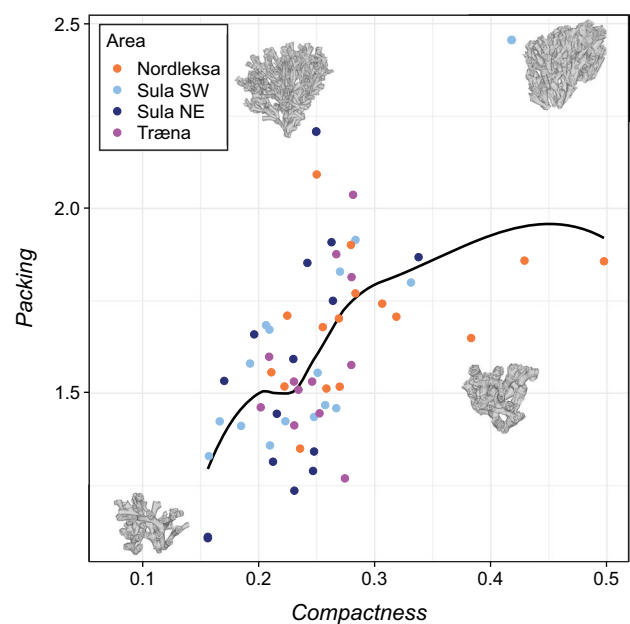

Fig. 4 Relationship between volume compactness and surface complexity of *Desmophyllum pertusum* colony samples, visualised on a scatter plot of *compactness* and *packing* with a LOESS smooth curve. Representative samples illustrate the range of variation in the two shape variables

Torchiano 2020) on both shape variables, log10-transformed to fulfil the normality assumption. Træna was not included in this part of the analysis, as it was representative of only a specific depth and, most likely, a single colony. To better understand the spatial scales and patterns of architectural variation, we compared intercolonial (between and within habitats) and intracolonial disparity in shape traits using the coefficient of variation (CV), a standardised measure of relative variability equal to the standard deviation divided by the mean, and often expressed as percentage. Specifically, we tested for differences in the CV of *compactness* and *packing* between study areas, before and after including Træna samples (thus accounting for intracolonial variation), using

the asymptotic test of Feltz and Miller (1996) included in the R package *cvequality* (Marwick and Krishnamoorthy 2019). All analyses were performed in R version 4.1.1 (R Core Team 2021), with an alpha level of 0.05. Plots were produced using the R packages *ggplot2* (Wickham 2016), *ggbeeswarm* (Clarke and Sherrill-Mix 2017) and *ggpubr* (Kassambara 2020).

Results

Compactness and *packing* were positively correlated (Spearman coefficient $r_s = 0.57$; $P < 0.00001$) (Fig. 4). Average values and CV of *compactness* and *packing* for each study area are shown in Table 1. ANOVA indicated statistically significant differences in *compactness* among Nordleksa, Sula SW and Sula NE ($F_{2,43} = 4.11$; $P = 0.023$). These were further explored with Tukey's test, which showed that pairwise differences were statistically significant only between Sula NE and Nordleksa (adjusted $P = 0.036$; Fig. 5), while they were non-significant between Sula SW and Nordleksa (adjusted $P = 0.058$) and between Sula NE and Sula SW (adjusted $P = 0.96$). Cohen's d (95% confidence interval) indicated that the largest difference in *compactness* was
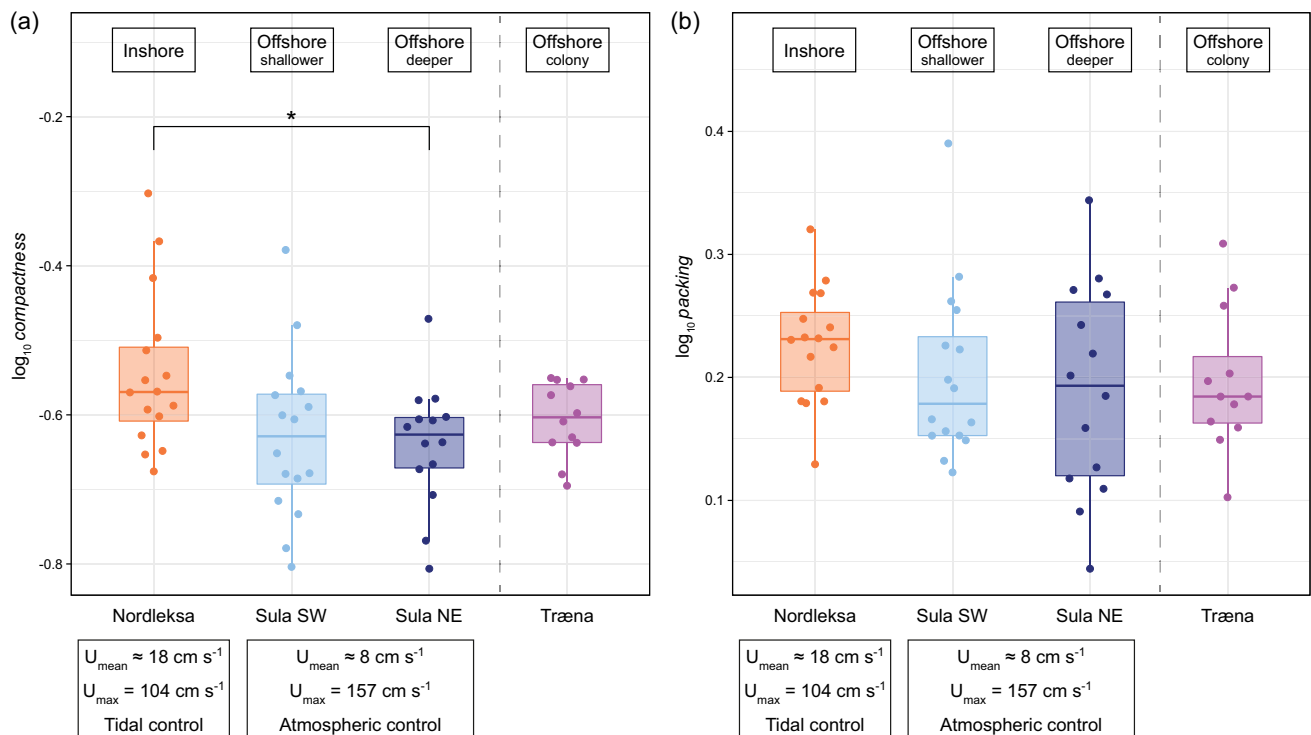
Table 1 Mean and coefficient of variation (CV) of *compactness* and *packing* for each study area. n = number of colony samples

Area	n	Compactness		Packing	
		Mean	CV (%)	Mean	CV (%)
Nordleksa	16	0.29	27.12	1.69	10.79
Sula NE	14	0.23	19.03	1.58	19.84
Sula SW	16	0.24	27.14	1.61	17.82
Træna	12	0.25	11.28	1.59	13.70

Fig. 5 Architectural variation of *Desmophyllum pertusum* colony samples between study areas with different flow regimes (U_{mean} = mean annual horizontal flow speed; U_{max} = peak horizontal flow speed). Volume compactness (**a**) and surface complexity (**b**) are described by log10-transformed *compactness* and *packing*, respectively, as used in the statistical analysis. Variation is summarised by boxplots indicating median (horizontal line enclosed by box), 1st and 3rd quartiles (lower and upper box hinges) and values within 1.5 × interquartile range (whiskers). Intracolonial samples from Træna were not included in the analysis, but are shown here for comparison

between Sula NE and Nordleksa ($d = 0.99$, 'large' effect), followed by the difference between Sula SW and Nordleksa ($d = 0.78$, 'medium' effect) and between Sula NE and Sula SW ($d = 0.11$, 'negligible' effect). Differences in *packing*, on the other hand, were not statistically significant among areas ($F_{2,43} = 1.12$; $P = 0.33$) and had lower effect sizes than *compactness* between habitats ($d_{\text{Sula NE–Nordleksa}} = 0.54$, 'medium' effect; $d_{\text{Sula SW–Nordleksa}} = 0.42$, 'small' effect; $d_{\text{Sula NE–Sula SW}} = 0.15$, 'negligible' effect). The asymptotic test indicated no statistically significant differences in the CV of *compactness* among Nordleksa and the two Sula areas ($P = 0.42$), while it yielded a statistically significant result ($P = 0.042$) when including intracolony samples from Træna. Differences in the CV of *packing* were statistically non-significant, both with ($P = 0.14$) and without the inclusion of Træna samples in the analysis ($P = 0.089$). Patterns of variation in volume compactness and surface complexity among study areas in relation to flow speed can be visually compared in the log10-transformed data of Fig. 5.

Discussion

Patterns and mechanisms of CWC architectural variation

We observed higher coral compactness in the higher-flow-speed fjord habitat at Nordleksa, in agreement with Büscher et al. (2019), but this difference was statistically significant only with respect to the deeper sector of the Sula offshore habitat (Sula NE). The more exposed Sula SW showed a relatively closer affinity to Nordleksa, which can be explained by the presence of more colonies at the high end of the volume compactness spectrum (Fig. 5a). Hence, there appears to be a joint effect of both sources of current speed variation considered here, i.e. habitat and local bathymetry, suggesting a strong hydrodynamic control on CWC architecture. However, this effect is seemingly restricted to volume compactness, because surface complexity did not differ significantly between habitats or offshore areas, despite the obvious geometric constraints that positively correlate the two traits (*compactness* and *packing* are both forms of convexity; Zawada et al. 2019a). Furthermore, while intracolonial variation in volume compactness was considerably lower than variation between and within habitats, surface complexity varied more consistently at all spatial scales analysed (Table 1 and Fig. 5b), as demonstrated by the asymptotic tests. Such contrasting patterns of variation seem to denote a trait-specific response of CWC colonies to flow speed, involving the architectural trait with the higher hydromechanical relevance, i.e. volume compactness.

We hypothesise that this decoupled trait response is enabled by the relatively simple colonial organisation of

Desmophyllum pertusum, compared to that of many shallow-water scleractinians (Coates and Jackson 1987). In fact, *D. pertusum* colonies are characterised by a fasciculate organisation with spaced corallites that represent the only modular level (Rosen 1986) and are free to grow rather independently due to such relaxed structural constraints. This low colony integration, along with intrinsic ontogenetic constraints (Gass and Roberts 2011), leads to high morphological disparity between individual corallites (Sanna and Freiwald 2021) and could therefore explain the high intracolonial variability in surface complexity. Volume compactness, on the contrary, is likely governed by the density of polyps and hence by their budding rate (Sanna and Freiwald 2021).

The high within-habitat and within-colony variation in both architectural traits (Table 1; Fig. 5) is probably contributed by phenotypic plasticity. Clonal propagation, in addition to asexual colony growth, may in fact constitute an important reef development mechanism for *D. pertusum*, with a few clones capable of having a broad spatial distribution within reefs (Dahl et al. 2012), although the extent of clonality can vary dramatically among different sites (Morrison et al. 2011; Becheler et al. 2017). Plasticity, in particular, likely plays a role in the comparable structural responses to water flow at Sula and Nordleksa, as they are in contrast with the marked genetic differentiation between the two populations (Le Goff-Vitry et al. 2004). This apparent architectural plasticity provides further evidence of a generally high acclimatisation potential of CWCs to environmental change (Form and Riebesell 2012), especially in the light of the trait-specific response we observed. Nevertheless, some adaptive morphological variation due to genetic differentiation is probably present within this species, perhaps not between the neighbouring fjord and offshore habitats analysed here, but rather at larger (e.g. interregional) scales, where morphotypes with strikingly different geometries occur (Sanna and Freiwald 2021).

Environmental influence on CWC architecture

Our results suggest a positive association between current speed and CWC framework compactness, which is in line with the responses known for zooxanthellate scleractinians and reflects trophic and mechanical factors with important implications for organismal fitness. Accelerated flow promotes enhanced food transport to CWC colonies, increasing encounter rates with food particles through their advection and resuspension (Genin et al. 1986; Davies et al. 2009). At the same time, a tightly branched framework effectively reduces the collateral hydromechanical stress (also through secondary branch fusion; Stetson et al. 1962) and slows flow down to speeds that are more favourable for polyp food capture (speeds < 7 cm s^{-1} are optimal for *D. pertusum*; Purser et al. 2010; Orejas et al. 2016), resulting in higher feeding

efficiency and higher energy budget for growth and reproduction (Hennige et al. 2021). Strong currents have indeed been linked to higher budding rates in *D. pertusum* (Chapron et al. 2020), as well as in the shallow-water scleractinian *Tubastraea* spp. (Tanasovici et al. 2022), which is also non-photosynthetic. Along with long-term flow regimes, CWC architecture could be affected by isolated strong current events. These are manifested at Sula by instantaneous flow speeds above 150 cm s^{-1} (see Fig. 2a in November 2013, for instance), which might contribute to the occurrence of highly compact colonies in this location (Fig. 5a), despite a considerably lower average flow speed than at Nordleksa. However, since growth of *D. pertusum* colonies entails tens to hundreds of years (Pons-Branchu et al. 2005; Brooke and Ross 2014), long-term flow conditions are probably more relevant for overall framework architecture.

Food supply, in the case of local topographic relief (addressed here by including two distinct Sula areas), may be enhanced not only by accelerated currents but also by increased vertical flux of particulate organic matter from the sea surface (Maier et al. 2021). In the more exposed Sula SW area, individual reefs are indeed larger and more abundant (Thorsnes et al. 2015, 2016), further suggesting higher food supply therein. It is important to note, however, that a compact architecture does not necessarily reflect optimal conditions for CWC growth. De Clippele et al. (2018), for instance, observed this at the Tisler Reef (Hvaler area, Norway): the proportion of short-branched *D. pertusum* colonies with a compact ("cauliflower") morphology was higher on the northwest side of the reef, which was exposed to a higher frequency of stronger currents (including the highest recorded speed at this site), while coral cover was much higher on the southeast side, where downwelling and food supply occurred more frequently in addition to more hard substrate being available. Strong currents can be a source of food, but also of mechanical damage for these relatively delicate branching colonies (Wilson 1979; Lim et al. 2020), and high branch density in response to high current speeds may lead to considerable food depletion in inner colony portions (Chamberlain and Graus 1975; Chang et al. 2009). Ultimately, CWC architecture probably represents a trade-off between adequate nutrition and structural integrity.

The local flow regime of a CWC reef habitat is influenced not only by seabed topography, but also by the corals themselves, which are capable of significantly altering the surrounding flow field with their complex structure, deflecting near-bed flow and decreasing turbulence and current speed in their wake (Mienis et al. 2019; Bartzke et al. 2021; Hennige et al. 2021; Corbera et al. 2022). This suggests that CWC colonies can mutually influence each other's morphology, by inducing heterogeneous flow patterns that may increase local architectural variability. In particular, highly compact colonies, by acting as a tight physical barrier, are likely to

reduce the exposure to fast flow and resources of sheltered downstream colonies, which as a result would grow with a less compact architecture. Nevertheless, this effect must be somewhat modulated by larger-scale changes in flow direction (Hennige et al. 2021), especially at Nordleksa, where regular tidal oscillations and turbulent flow are important components of the benthic current regime and food supply mechanisms (Juva et al. 2020). Flow direction has indeed shown to be an important driver of morphology in deep-water octocorals of the genus *Paragorgia*, which develop a concave fan shape when exposed to strong unidirectional currents, maximising food intake and resistance to hydrodynamic forces, as opposed to non-concave colonies occurring in different flow conditions (e.g. turbulent flow closer to the bottom) (Mortensen and Buhl-Mortensen 2005; Morato et al. 2021). Variation in overall colony shape in response to currents was suggested to also occur in *D. pertusum* (which can acquire an asymmetrical fan shape too; Sanna and Freiwald 2021) and would represent a morphological response complementary to the architectural strategies observed here.

Fine-scale flow patterns at the colony level might actually represent a key driver of surface complexity, because they modulate differential resource acquisition among polyps, which is closely linked to surface area (Kim and Lasker 1998). This would explain the high intracolonial variability in surface complexity and would imply that the effect of water motion on CWC architecture is not only trait-specific, but also scale-dependent, with surface complexity being affected exclusively at the microhabitat scale. Characterisation of in situ reef flow patterns at the colony and patch scale (cm to m), which are still poorly known (Mienis et al. 2019), is needed to advance our understanding of the effects of water motion on CWC morphology. A more detailed quantification of the relationship between ambient currents and CWC architecture could enable, for instance, the use of *compactness* as a proxy for flow speed, also in the fossil record, with implications for palaeoenvironmental reconstruction. High local architectural variability and the use of average reef flow speed prevent such quantitative inferences in this study, although very high *compactness* values (e.g. > 0.30) could arguably be considered a reliable indicator of a CWC habitat with relatively strong currents.

Although limitedly divergent between the studied habitats, other hydrological parameters could influence framework architecture by interacting in complex ways with hydrodynamics, given the fact that coral calcification is jointly affected by several environmental factors (Tambutté et al. 2011). Flow patterns, for instance, can considerably alter bottom water temperature (Guihen et al. 2012). Denser colony growth at Nordleksa might be further promoted by its slightly higher temperature, as laboratory experiments have shown that *D. pertusum* growth rates increase in response to a combination of higher temperatures and higher food supply

(Büscher et al. 2017), and an analogous combination leads to increased growth and budding rates in the Mediterranean scleractinian *Cladocora caespitosa* (Rodolfo-Metalpa et al. 2008). Moreover, while average physicochemical parameters are rather consistent between Nordleksa and Sula, they show large seasonal variability within both sites (Büscher et al. in prep.), which, along with variability at broader temporal scales, might be related to local architectural diversity. Interspecific interactions can also alter *D. pertusum* skeletal morphology (Freiwald and Wilson 1998; Beuck et al. 2007), although the signs of ubiquitous presence of the important symbiont *Eunice norvegica* in our samples suggest a minor influence on colony architectural traits. Nevertheless, environmental (abiotic or biotic) factors that have limited influence on the architecture of CWCs may still be highly relevant for their structural integrity, by affecting internal skeletal properties (e.g. porosity) and thus the ultimate framework strength (Hennige et al. 2020; Wolfram et al. 2022). Therefore, the interplay between multiple factors should be considered when trying to predict CWC net responses to environmental change.

Ecosystem significance of CWC architectural variation

The marked architectural diversity of *D. pertusum* at local scales has important implications for CWC reef ecosystems, suggesting partitioning of the coral's ecological functions not solely among different reef zones (living coral, dead framework and coral rubble; Freiwald et al. 2004), but also between different portions of the dead framework. In terms of habitat provision, this architectural variability may induce locally heterogeneous distribution patterns of reef-dwelling organisms that thrive in different framework configurations, contributing to complex local structuring of CWC reef communities (Henry et al. 2013). Architectural differences between fjord and offshore reefs could partly underpin the recognised differences in community composition between these habitats, but it is difficult to establish a causal link. For instance, Mortensen and Fosså (2006) observed higher diversity of coral-associated invertebrates in mid-Norwegian inshore reefs (including Nordleksa) compared to reefs at Sula. This pattern is consistent with the higher surface complexity of Nordleksa corals (although statistically non-significant) but in contrast with their higher volume compactness (Table 1; Fig. 5), because generally surface complexity creates niches for other organisms while compactness reduces them (Zawada et al. 2019b). A possible reason for the diversity pattern observed by Mortensen and Fosså (2006) might be the preference of some invertebrate species for tightly branched coral hosts, which ensure better protection, especially to smaller individuals (Vytopil and Willis 2001), but there is no doubt that several other ecological determinants of community assembly are involved

(Pearson 1980). Even with regard to coral structures alone, habitat provision could also be affected by aspects not considered in this study, such as colony size, framework continuity and whole-reef geometry.

Local architectural variation might also play a role in CWC reef and mound formation, by regulating baffling, settling and interstitial accumulation of sediment in the coral framework. In principle, more compact *D. pertusum* colonies intercept sinking and transported sediment more effectively and require a lower amount of infill, becoming buried more rapidly and thus enhancing reef and mound growth rates under suitable sediment supply conditions (Wang et al. 2021). CWC growth, hydrodynamics and sedimentation are mutually influenced at multiple scales, with development of colonies, reefs and mounds enhancing flow, food supply to living colonies and sediment baffling by dead framework, and thus further growth (Masson et al. 2003; Davies et al. 2009; Buhl-Mortensen et al. 2016; van der Kaaden et al. 2021; Corbera et al. 2022). The high sensitivity of CWC architecture to water flow may further boost this positive feedback mechanism, with exposure of elevated colonies to stronger currents (and enhanced food supply) resulting in higher compactness, which would in turn facilitate post-mortem sedimentary infilling. This hypothesis is supported by observations of morphological variation matching reef zonation at Sula (Mortensen et al. 1995; Freiwald et al. 2002) and at the Stjernsund Reef (Finnmark, Norway) (Freiwald et al. 1997). Enhanced sediment baffling by more compact framework would also increase reef nutrient cycling, as the fine baffled sediment includes particulate organic matter (de Froe et al. 2019) which contributes significantly to carbon turnover in CWC reefs (De Clippele et al. 2021). This effect might be further modulated by architecture-driven changes in diversity and abundance of the framework-dwelling organisms, also involved in nutrient (re)cycling (Maier et al. 2021).

In order to improve our comprehension of the full spectrum of effects that global environmental change can have on CWC ecosystem functioning and services, we argue it is crucial to further investigate not only the response of CWC morphological traits to the environment, but also their effects on reef ecosystem processes.

Declarations

Conflict of interest   The authors have no competing interests to declare.

Data availability   3D models and morphological data generated and analysed during the current study are available from Figshare: https://doi.org/10.6084/m9.figshare.20278602.

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