


On the paradox of thriving cold-water coral reefs in the food-limited deep sea

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ABSTRACT

The deep sea is amongst the most food-limited habitats on Earth, as only a small fraction (<4%) of the surface primary production is exported below 200 m water depth. Here, cold-water coral (CWC) reefs form oases of life: their biodiversity compares with tropical coral reefs, their biomass and metabolic activity exceed other deep-sea ecosystems by far. We critically assess the paradox of thriving CWC reefs in the food-limited deep sea, by reviewing the literature and open-access data on CWC habitats. This review shows firstly that CWCs typically occur in areas where the food supply is not constantly low, but undergoes pronounced temporal variation. High currents, downwelling and/or vertically migrating zooplankton temporally boost the export of surface organic matter to the seabed, creating 'feast' conditions, interspersed with 'famine' periods during the non-productive season. Secondly, CWCs, particularly the most common reef-builder *Desmophyllum pertusum* (formerly known as *Lophelia pertusa*), are well adapted to these fluctuations in food availability. Laboratory and *in situ* measurements revealed their dietary flexibility, tissue reserves, and temporal variation in growth and energy allocation. Thirdly, the high structural and functional diversity of CWC reefs increases resource retention: acting as giant filters and sustaining complex food webs with diverse recycling pathways, the reefs optimise resource gains over losses. Anthropogenic pressures, including climate change and ocean acidification, threaten this fragile equilibrium through decreased resource supply, increased energy costs, and dissolution of the calcium-carbonate reef framework. Based on this review, we suggest additional criteria to judge the health of CWC reefs and their chance to persist in the future.

Key words: trophic interaction, carbon, nitrogen, respiration, recycling loop, ecosystem engineer, organic matter, cold-water coral reef, climate change, food web.

CONTENTS

I. Introduction	1769
II. Food supply to cold-water coral reefs	1774
(1) Are cold-water coral reefs limited to locations with elevated food supply?	1774
(2) Food pulses created by hydrodynamic processes	1776
(3) Seasonal variability of food pulses	1778
(4) The role of live zooplankton	1779

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III. Adaptations of cold-water corals to the feast–famine environment	1779
IV. How do cold-water coral reefs sustain their high food demand?	1782
(1) The reef filter	1782
(2) Recycling of metabolic ‘waste’ products	1782
V. Perspectives: cold-water coral reefs in the anthropocene	1785
(1) Disbalanced energy budget of cold-water corals	1785
(2) Reduced reef functioning on ‘crumbling’ reefs	1787
(3) Conservation of cold-water coral reefs in the Anthropocene	1787
VI. Conclusions	1788
VII. Acknowledgements	1788
VIII. References	1788
IX. Supporting information	1795

I. INTRODUCTION

The deep sea is the largest habitat on Earth, located below the continental shelf break from *ca.* 200 m water depth (Ramirez-Llodra *et al.*, 2010, 2011). Here, far below the productive waters at the ocean surface, cold-water corals (CWCs, Fig. 1) form reefs of surprisingly high biodiversity, biomass, and metabolic activity (Fig. 2, Freiwald *et al.*, 2004; Roberts, Wheeler & Freiwald, 2006; Cathalot *et al.*, 2015; De Clippele *et al.*, 2021a).

CWCs encompass different taxonomic groups within the classes Hexacorallia, Octocorallia (*sensu* McFadden, Ofwegen & Quattrini, 2022), and Hydrozoa. In contrast to their well-known warm-water relatives, CWCs occur at relatively low temperatures (i.e. <14 °C for reef-building CWCs; Freiwald *et al.*, 2004; Gómez *et al.*, 2022), facilitating an almost global distribution in the deep sea (i.e. >200 m water depth, Fig. 3A). However, they can also occur at shallower depths, e.g. at 36 m depth in Norwegian fjords, when oceanographic conditions are suitable. Many CWCs create structurally complex and diverse ‘marine animal forests’ (reviewed by Rossi *et al.*, 2017), including soft coral (Octocorallia) gardens (e.g. Long *et al.*, 2020; Schejter *et al.*, 2020), black coral (Antipatharia) gardens (e.g. Rakka *et al.*, 2017, 2020), lace coral (Stylasteridae) gardens (e.g. Di Camillo *et al.*, 2017), and stony coral (Scleractinia) reefs. In this review, we focus on scleractinian CWCs that can form or contribute to large, long-lasting carbonate reefs in the deep sea (Table 1). Small coral polyps (<1 cm diameter; Filander *et al.*, 2021) secrete an aragonite (calcium carbonate) skeleton and together can form ~1.5 m-high CWC colonies (Fig. 1; Wilson, 1979). Live polyps are restricted to the upper and outer parts of the colonies, as coral polyps in the inner parts become shaded from food-delivering currents and die (Fig. 2; Wilson, 1979; Mortensen & Fosså, 2006; Hennige *et al.*, 2021). The carbonate skeleton becomes exposed to physical and biological erosion (Beuck & Freiwald, 2005), which causes fragments to break off and develop into new colonies around the original colony (Fig. 2). The extending coral framework traps mobile (e.g. resuspended) sediment, leading to framework cementation and formation of elevated, kilometres-long CWC reefs

(Dorschel *et al.*, 2005; Roberts *et al.*, 2006). Over time, CWCs develop large carbonate structures such as the CWC mounds at Rockall Bank in the North East Atlantic, which are 300 m high and thousands to millions of years old (Roberts *et al.*, 2006).

The topologically complex reef framework, especially the ‘dead’ skeleton, provides habitat, feeding grounds and spawning/nursery areas for a variety of associated species (Fig. 2), including sessile suspension feeders, such as sponges, other corals, and bivalves (Jonsson *et al.*, 2004; Mortensen & Fosså, 2006; Henry & Roberts, 2007, 2016; Cordes *et al.*, 2008), mobile invertebrates, and commercially and socio-economically valuable fish (Costello *et al.*, 2005; Henry *et al.*, 2013; Kutti *et al.*, 2014). Furthermore, a diverse microbial community grows on and inside the reef framework and associated with reef animals such as sponges and corals (Schöttner *et al.*, 2012, 2013; Cardoso *et al.*, 2013; van Bleijswijk *et al.*, 2015). The biodiversity of CWC reefs is on a par with tropical shallow-water coral reefs (Jonsson *et al.*, 2004; Mortensen & Fosså, 2006; Henry & Roberts, 2007) and directly benefits humanity, e.g. through the provision of fisheries species for food and biotechnological resources for drug development (Rocha *et al.*, 2011; Armstrong *et al.*, 2014). Moreover, the reefs form hotspots of biomass, metabolic activity, and carbon (C) and nitrogen (N) turnover in the deep sea (van Oevelen *et al.*, 2009; Cathalot *et al.*, 2015; De Froe *et al.*, 2019; De Clippele *et al.*, 2021a,b). Due to their high organic matter retention and biomass, CWC reefs have the potential to sequester C for decades to centuries (Dorschel *et al.*, 2007; Titschack *et al.*, 2009; Coppari, Zanella & Rossi, 2019).

The high biodiversity, biomass and metabolic activity of CWC reefs appear paradoxical, as the deep seafloor belongs to the most food-limited habitats on Earth (Ramirez-Llodra *et al.*, 2010). Due to the absence of light, CWCs lack zooxanthellae (Freiwald *et al.*, 2004), i.e. symbiotic dinoflagellates that contribute to the nutrition of most reef-building shallow-water corals (Goldberg, 2013). Like most deep-sea benthos, CWCs depend on organic matter produced in the sunlit surface waters, such as phytodetritus (remains of phytoplankton), zooplankton, and zooplankton remains (e.g. dead

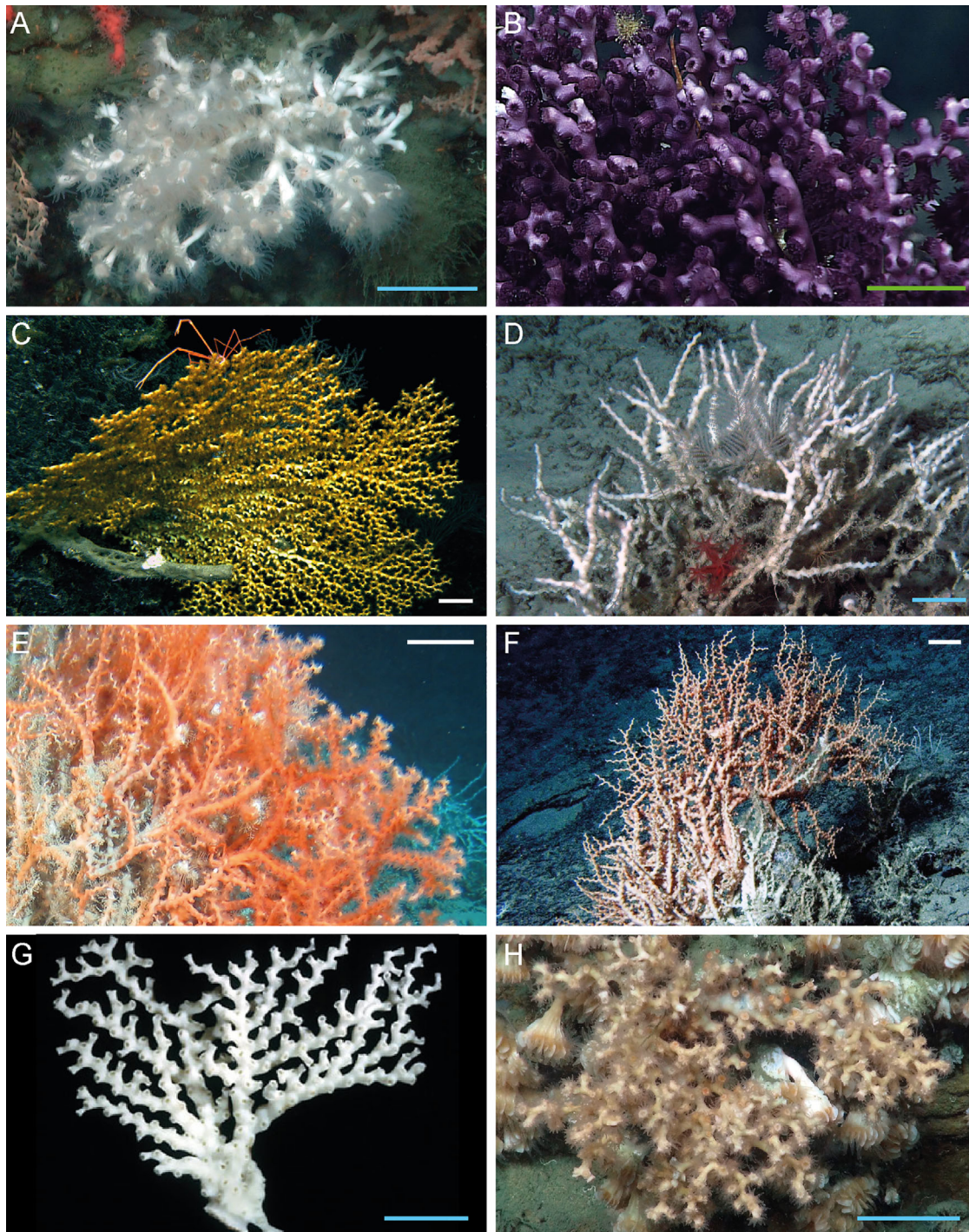


Fig. 1. Reef-forming or structure-forming cold-water corals (CWCs) (see Table 1). (A) *Desmophyllum pertusum* colony on the wall of Baltimore Canyon, Western Atlantic (434 m). Credit: Deepwater Canyons 2012 Expedition NOAA-OER/BOEM/USGS. (B) *Enallopsammia* cf. *pusilla* from the Hawaiian Seamounts (~800 m). Credit: NOAA-OER, 2015 Hohonu Moana. (C) *Enallopsammia rostrata* colony on the deep wall of the West Florida Escarpment (1900 m). Credit: Brooke *et al.* (2022), NOAA-OER/ROV Global Explorer. (D) *Enallopsammia profunda* from the coral mounds of the southeastern USA (770 m). Credit: Brooke *et al.* (2005), NOAA-OE. (E) *Madrepora oculata* from the coral mounds off Cape Canaveral, Florida (420 m). Credit: Ross & Quattrini (2009); NOAA DSCRTP/CIOERT/USGS. (F) *Madrepora oculata* colony on exposed rocky habitats of the Florida Straits, USA (400 m). Credit: Brooke *et al.* (2005), NOAA-OE. (G) *Madrepora carolina* colony collected from the Rosalind Bank, Nicaragua (162 m). Credit: Stephen Cairns, Smithsonian Institute of Natural History, USA. (H) *Solenosmilia variabilis* with individual, larger polyps of *Desmophyllum dianthus* on the wall of Norfolk Canyon, Western Atlantic (1200 m). Credit: Deepwater Canyons 2013 Expedition NOAA-OER/BOEM/USGS. Scale bars, green: 1 cm, blue: 5 cm, white: 10 cm.

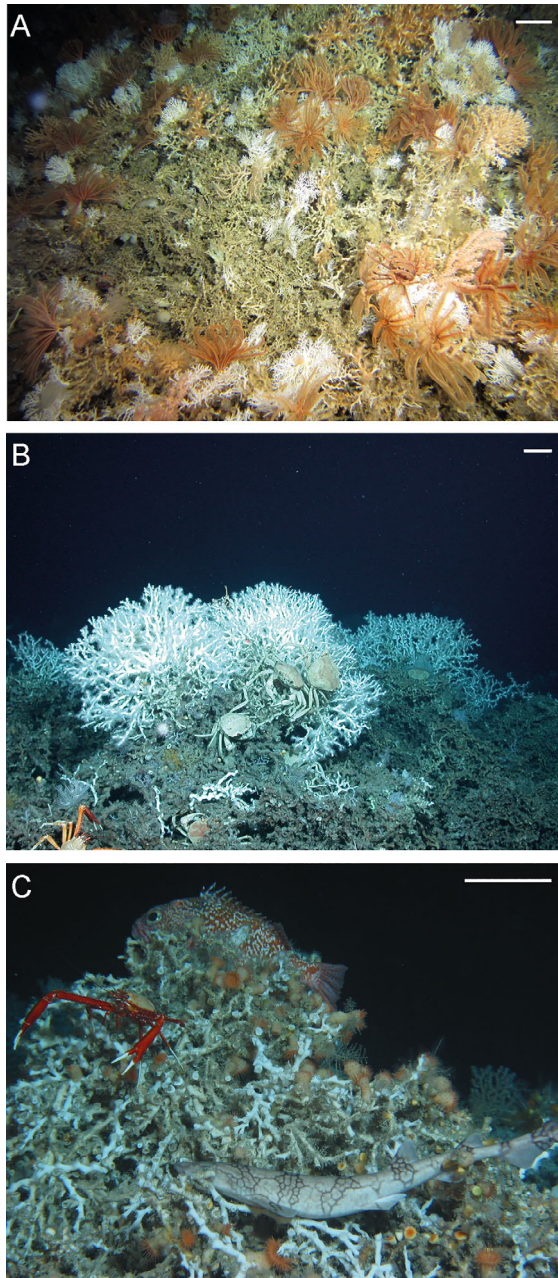


Fig. 2. Cold-water coral (CWC) reefs, hotspots of biodiversity. (A) Reef framework formed by *Desmophyllum pertusum* and *Madrepora oculata* on the Oreo CWC Mound (summit: 750 m depth), SE slope of Rockall Bank, NE Atlantic; large crinoids (orange) and stylasterid corals (white) live on the reef framework. Credit: Research cruise 64PE4202F. (B) Large colonies of *D. pertusum* on the West Florida Slope; these mounds provide habitat for golden crabs (*Chaceon fenneri*), which are fished commercially in the southeastern USA (567 m). Credit DISCOVRE expedition 2010 USGS/BOEMRE. (C) Live and dead structure of a *D. pertusum* colony off Cape Canaveral, Florida (430 m) with a blackbelly rosefish (*Helicolenus dactylopterus*) on the top of the colony, a galatheid crab (*Eumunida picta*) and a Chain Catshark (*Scyliorhinus cf. retifer*). Credit: Ross & Quattrini (2009), NOAA DSCRTP/CIOERT/USGS. Scale bars (top of images): 10 cm.

zooplankton, faecal pellets) (Duineveld, Lavaleye & Berghuis, 2004; Duineveld *et al.*, 2007; Naumann *et al.*, 2015; van Oevelen *et al.*, 2018). Phytodetritus and zooplankton faecal pellets aggregate and slowly sink from the photic zone to the deep sea as exported particulate organic matter (POM) (Turner, 2015). In addition, live zooplankton perform diurnal and/or seasonal vertical migrations between shallow and deep waters (Bandara *et al.*, 2021). As passive suspension feeders, CWCs require currents to deliver food particles (Hamann & Blanke, 2022), which they capture with their tentacles or with mucus nets (Zetsche *et al.*, 2016; Murray *et al.*, 2019).

With increasing depth, the vertical flux of particulate organic carbon (POC) decreases exponentially (Fig. 4A), as zooplankton and bacterioplankton consume a substantial fraction of the sinking organic material (Suess, 1980; Lutz, Dunbar & Caldeira, 2002; Boyd & Trull, 2007). In the North Atlantic, 2.5 to 10 mol POC m⁻² year⁻¹ is exported from the photic zone in coastal areas, but only around 0.1 mol POC m⁻² year⁻¹ (1–4%) arrives in the bathyal deep sea (>200 m; Fig. 4A, see online Supporting Information, Table S1). On CWC reefs, 0.0003–3.5 mol POC m⁻² year⁻¹ are deposited, as measured by sediment traps deployed at 481–850 m water depth (Fig. 4A). At the same time, CWC reefs respire 4–45 mol oxygen m⁻² year⁻¹, up to 20 times more than adjacent soft-sediment communities [respiration rates extrapolated from daily measurements of reef-community oxygen consumption on different reefs in the North Atlantic during spring/summer (Cathalot *et al.*, 2015; De Froe *et al.*, 2019)]. Assuming a respiratory quotient CO₂:O₂ of 1 (as estimated for CWCs; Khripounoff *et al.*, 2014), this leads to a C turnover of 4–45 mol C m⁻² year⁻¹ (Fig. 4B; note that C refers to organic C throughout this review). To sustain this high C turnover, the reefs require an amount C that is orders of magnitude higher than the amount of POC deposited in sediment traps (Fig. 4B). The reefs even seem to require a substantial part of the entire primary production at the ocean surface [almost 100% of the local primary production above Mingulay Reef (De Clippele *et al.*, 2021a); 5% of the primary production on the entire Norwegian shelf by all known Norwegian reefs combined (Cathalot *et al.*, 2015)]. This poses the question: how can CWC reefs sustain their high biomass and metabolic activity in the food-limited deep sea, given this apparent mismatch in C supply (Fig. 4B)?

To approach this ‘CWC reef paradox’, we review the literature and open-access data and discuss the following questions: are CWC reefs limited to locations with elevated food supply, and what mechanisms increase the food supply to the reefs (Section II); how are CWCs adapted to their food environment (Section III); how do CWC reefs function as ecosystem to maintain high metabolic rates (Section IV); and how do anthropogenic threats impact food supply, coral adaptations and reef functioning and jeopardise the existence of CWC reefs; from a trophodynamic perspective, how can we optimally protect CWC reefs? (Section V).

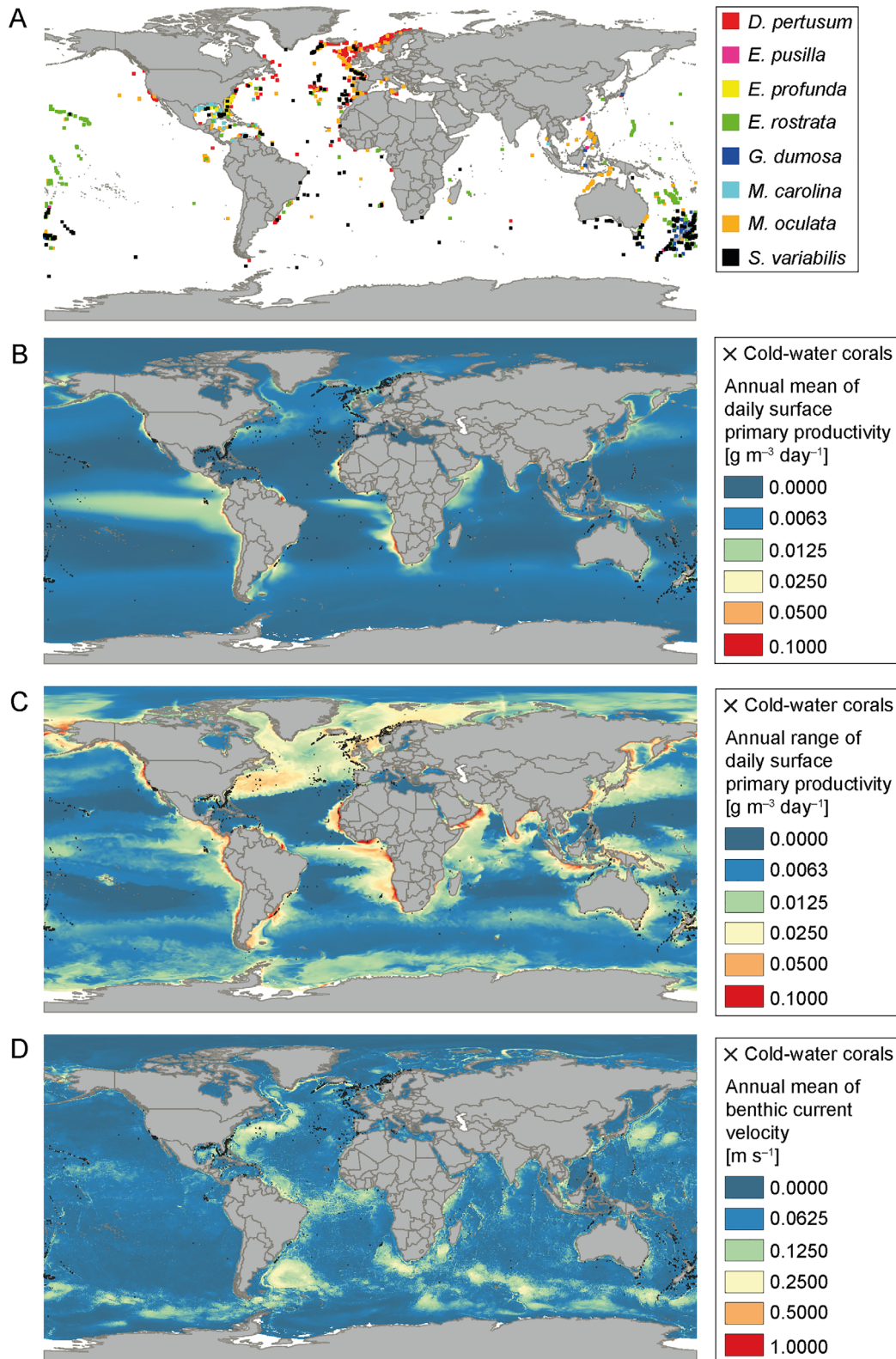


Fig. 3. Cold-water coral (CWC) occurrence, surface productivity and benthic current velocity. Data from OBIS (2022) and Bio_ORACLE (Tyberghein *et al.*, 2012; Assis *et al.*, 2018). (A) Global occurrence of *Desmophyllum pertusum*, *Enallopsammia pusilla*, *Enallopsammia profunda*, *Enallopsammia rostrata*, *Goniocorella dumosa*, *Madrepora carolina*, *Madrepora oculata*, and *Solenosmilia variabilis*. (B) Annual mean of daily surface primary productivity. (C) Annual range of daily surface primary productivity. (D) Annual mean of benthic current velocity. A QGIS version of B–D can be found at <https://doi.org/10.5281/zenodo.7097065>.

Table 1. Colonial, reef-building and/or structure-forming cold-water coral (CWC) species, their colony morphology, the degree to which they are reef-building, their distribution, depth range (mean \pm standard deviation), and the number of publications mentioning each species (*Google Scholar*, 01 September 2022). All species are cnidarians of the order Scleractinia. Only species that occur at >200 m water depth were considered. References for presented information: Zibrowius (1980); Cairns (1982, 1995); Koslow *et al.* (2001); Reed (2002); Freiwald *et al.* (2004); Hebbeln *et al.* (2014); De Clippele *et al.* (2017b); Corbera *et al.* (2019); Raddatz *et al.* (2020); Filander *et al.* (2021); Sanna & Freiwald (2021); OBIS (2022) and <https://doi.org/10.5281/zenodo.7097065>.

Species	Colony morphology	Reef-building	Distribution	Depth range (m water depth)	Number of publications mentioning species
<i>Desmophyllum pertusum</i> (formerly <i>Lophelia pertusa</i> ; Linnaeus, 1758)	Bushy/bush-like to cauliflower-shaped	Dominant reef-building CWC in North Atlantic	Almost cosmopolitan (not found in continental Antarctica)	480 \pm 184	' <i>Lophelia pertusa</i> : 6630; <i>Desmophyllum pertusum</i> : 270
<i>Goniocorella dumosa</i> (Alcock, 1902)	Bushy	Dominant reef-building CWC around New Zealand	Only Southern hemisphere	462 \pm 239	198
<i>Enallopsammia rostrata</i> (Pourtales, 1878)	Fan-shaped, uni-planar	Mostly secondary framework producer on reefs formed by other species, but some can also build reefs (<i>E. profunda</i> , <i>M. oculata</i> , <i>S. variabilis</i> ; the others are considered 'structure-forming')	Almost cosmopolitan (not found in continental Antarctica)	763 \pm 338	487
<i>Enallopsammia profunda</i> (Pourtales, 1867)	Irregular-fragile			667 \pm 212	173
<i>Enallopsammia pusilla</i> (Alcock, 1902)	Bushy			568 \pm 233	12
<i>Madrepora oculata</i> (Linnaeus, 1758)	Uniplanar zigzag-shaped branches			654 \pm 307	2530
<i>Madrepora carolina</i> (Pourtales, 1871)	Fan-shaped, uni-planar			225 \pm 218	68
<i>Solenastrea variabilis</i> (Duncan, 1873)	Bushy		Almost cosmopolitan (not found in continental Antarctica & North Pacific)	1258 \pm 276	721

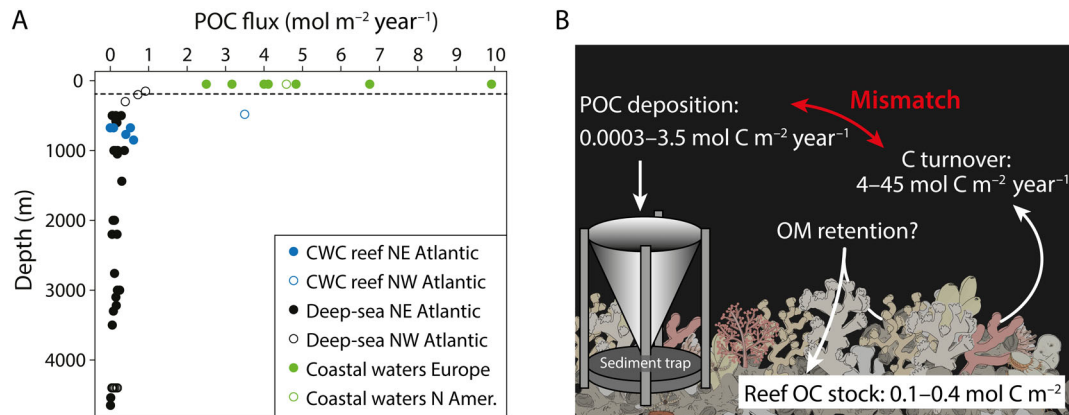


Fig. 4. Paradox of thriving cold-water coral (CWC) reefs in the food-limited deep sea. (A) Organic matter export from the ocean surface to the deep sea, measured by sediment traps, plotted as annual flux of particulate organic carbon (POC) over depth. Green symbols show POC export from the photic zone (data from coastal water, 50 m water depth; export flux data from directly above CWC reefs are lacking); black symbols show off-shelf POC flux through the water column (data from moored sediment traps); blue symbols show POC flux close to cold-water coral (CWC) reefs (data from sediment traps on benthic landers). Dashed line indicates transition from photic zone to deep sea at 200 m water depth. (B) Simplified organic carbon (OC) budget of CWC reefs, illustrating the mismatch between high C turnover, high OC stock in reef biomass, and low POC deposition measured by sediment traps. OM, organic matter. References for (A): Wassmann (1990); Antia *et al.* (2001); Bermuda Atlantic Time-series Study (BATS), see Steinberg *et al.* (2001); Smith & Rabouille (2002); Duineveld *et al.* (2004); Lavaley *et al.* (2009); Mienis *et al.* (2009, 2012); van Oevelen *et al.* (2009); Khrifounoff *et al.* (2014). Data set summarised in Table S1. References for B: POC deposition as in A; C turnover: Cathalot *et al.* (2015); De Froe *et al.* (2019) and references therein; Reef OC stock: De Clippele *et al.* (2021b).

II. FOOD SUPPLY TO COLD-WATER CORAL REEFS

(1) Are cold-water coral reefs limited to locations with elevated food supply?

CWCs are supplied with food through primary production at the ocean surface (measured as chlorophyll-*a* concentration or net primary productivity), export of primary production, flux of POM to the seafloor and/or currents (horizontal and/or vertical) that carry food particles (e.g. Duineveld *et al.*, 2004; Kiriakoulakis *et al.*, 2004, 2007; Davies *et al.*, 2009; De Froe *et al.*, 2022). To evaluate whether CWC reefs are limited to locations with elevated food supply, we first reviewed modelling studies that predict habitat suitability for reef-building/structure-forming CWCs (Table 1), based on their environmental requirements including ‘food supply’ (primary production, export, POC flux and/or current velocity; Table 2). Currents were identified as an important predictor of CWC habitat suitability in nine out of 13 models that explicitly included currents (Table 2). The importance of surface primary production and/or POM flux varied between the habitat suitability studies: 40% of the 30 relevant models (i.e. models that included the relevant parameters) describe the importance of primary production/POC flux as (relatively) high, 27% as moderate, and 33% as (relatively) low.

Secondly, we carried out a global analysis to test specifically whether surface primary productivity and/or benthic

current velocity were above global average at those sites where either of the eight reef-building/structure-forming deep-sea CWC species (Table 1) occur. Publicly available data on the occurrence of these were obtained from OBIS (2022; data sets are available at <https://doi.org/10.5281/zenodo.7097065>). Raster layers with values for (i) the annually averaged surface primary productivity; (ii) the annual range of surface primary productivity as an indicator of seasonality; and (iii) the annually averaged current velocity were extracted from Bio-ORACLE (Tyberghein *et al.*, 2012; Assis *et al.*, 2018; resolution 5 arcmin, i.e. ca. 9.2 km at equator). Bio-ORACLE compiles a global environmental data set for species distribution modelling, based on data sets provided by the E.U. Copernicus Marine Service Information (Assis *et al.*, 2018). For a detailed description of the methodology, see online supporting information Appendix S1; the full R code for all analyses is available at <https://doi.org/10.5281/zenodo.7097065>.

Our global analysis revealed that enhanced food supply through above-average surface productivity and currents drive the distribution of most reef-forming CWC species. Firstly, five out of eight species (i.e. *Desmophyllum pertusum*, *Enallopsammia profunda*, *Goniocorella dumosa*, *Madrepora oculata*, *Solenosmilia variabilis*) occur in locations with higher primary productivity than the global average (Figs 3B and 5A, Table 3, Appendix S2). Some species, however, occur in areas of non-enhanced (*Enallopsammia pusilla*, *Enallopsammia rostrata*) or even lower (*Madrepora carolina*) primary

Table 2. Environmental parameters that best predict suitable habitat for deep-sea scleractinian cold-water corals (CWCs). The table includes only studies that explicitly analysed CWCs or CWC species (not CWC reefs) in relation to food availability ('food parameter') and/or currents. From these studies, the most important 'predictors' are listed, i.e. those environmental parameters that best predict the habitat suitability of CWCs: arag, aragonite saturation; aspect, easterly & northerly aspect; BPI, bathymetric positioning index; DIC, dissolved inorganic carbon concentration; nutrients, concentration of nitrate, phosphate, (silicate); O₂, oxygen concentration; rugg, terrain ruggedness; S, salinity; seamount, association with a seamount; shear, bottom shear stress; SST, sea surface temperature; T, temperature; TA, total alkalinity; terrain, combined terrain parameters; v, current velocity; all parameters refer to bottom-water/seafloor, unless otherwise indicated. Food parameters are: chl-a, chlorophyll-a concentration at ocean surface; DOM flux, dissolved organic matter flux to the seafloor; export PP, export primary productivity; NPP, net primary productivity; POC flux, particulate organic matter flux to the seafloor. Studies where food availability and/or current velocity were important predictors are highlighted in grey.

Study	Species	Region	Scale	Most important predictors	Food parameter	Importance of food as predictor	Importance of currents as predictor
Davies <i>et al.</i> (2008)	<i>D. pertusum</i>	Global	Global	TA, aspect, arag, DIC	chl-a	Moderate to high	High
Titensor <i>et al.</i> (2009)	Scleractinia (pooled)	NE Atlantic	Regional	Aspect, depth, slope		Moderate	Relatively high
Davies & Guinotte (2011)	<i>D. pertusum</i> <i>E. rostrata</i> <i>G. damosa</i> <i>M. oculata</i> <i>S. variabilis</i>	Global	Global features	arag, O ₂ , nutrients, DIC	Export PP, NPP	Low	Low
Tracy <i>et al.</i> (2011)	<i>E. rostrata</i>	New Zealand	Regional	S, T, arag Depth, T, arag Depth, T, arag Depth, T, arag Depth, T, arag POC flux, DOM, depth	POC flux	Moderate	NA
Rengstorf <i>et al.</i> (2013)	<i>G. damosa</i> <i>M. oculata</i> <i>S. variabilis</i> <i>D. pertusum</i> reef	Irish continental margin, NE Atlantic	Local	Depth, seamount Seamount, DOM Depth, seamount Slope, T, shear	POC flux, DOM flux	High	High
Georgian <i>et al.</i> (2014)	<i>D. pertusum</i>	Gulf of Mexico	Regional	Hard substrate, depth, BPI	POC flux	Low	High [vertical & bottom shear stress]
Rengstorf <i>et al.</i> (2014)	<i>D. pertusum</i> framework	CWC provinces, NE Atlantic	Local	Shear, BPI, slope, vertical flow	NA		High [bottom shear stress]
De Clippele <i>et al.</i> (2017a)	<i>D. pertusum</i> reef	Mingulay Reef Complex, NE Atlantic	Local	Depth, rugosity, BPI, v	NA		Relatively high
Bargain <i>et al.</i> (2018)	<i>D. pertusum</i> <i>M. oculata</i>	Mediterranean Sea canyons	Regional features	rugg, BPI, v, T	NA		High
Chu <i>et al.</i> (2019)	Scleractinia (pooled)	Canadian NE Pacific	Regional	O ₂ , SST, arag	chl-a	Relatively low	Moderate [vertical & horizontal]
Georgian <i>et al.</i> (2019)	<i>E. rostrata</i> <i>G. damosa</i> <i>M. oculata</i> <i>S. variabilis</i>	New Zealand + adjacent S Pacific	Regional	T, rugg, arag T, arag, rugg BPI, arag, T rugg, arag, % gravel	POC flux	Relatively low	NA
Barbosa <i>et al.</i> (2020)	<i>D. pertusum</i> <i>E. rostrata</i> <i>M. oculata</i> <i>S. variabilis</i>	Brazilian continental margin, W Atlantic	Regional	Depth, T, arag Depth, arag, T Depth, T, arag S, depth, POC flux	POC flux	Relatively low	Relatively high [vertical]

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Table 2. (Cont.)

Study	Species	Region	Scale	Most important predictors	Food parameter	Importance of food as predictor	Importance of currents as predictor
Burgos <i>et al.</i> (2020)	<i>D. pertusum</i> <i>M. oculata</i> <i>S. variabilis</i>	Nordic Seas (Norway Sea, Greenland Sea, Icelandic Sea, part of Barents Sea)	Regional	T, depth, terrain T, terrain, depth Depth, T, v	POC flux, NPP	Relatively high Low Low	Relatively low Relatively low Relatively high
Kinlan <i>et al.</i> (2020)	<i>Scleractinia</i> (pooled)	US continental shelf, NW Atlantic	Regional	T, depth, chl-a	chl-a	High	M
Morato <i>et al.</i> (2020)	<i>D. pertusum</i> <i>M. oculata</i>	N Atlantic	Regional	T, POC flux, arag T, POC flux, arag	POC flux	High High	M
Sundahl <i>et al.</i> (2020)	<i>D. pertusum</i>	Norwegian continental shelf	Regional	BPI, sediment, T, v	chl-a	Relatively high	High
Georgian <i>et al.</i> (2021)	<i>Scleractinia</i> (pooled)	S Pacific off Peru	Regional	Arag, BPI, rugg, nutrients, POC flux	POC flux	Relatively high	M

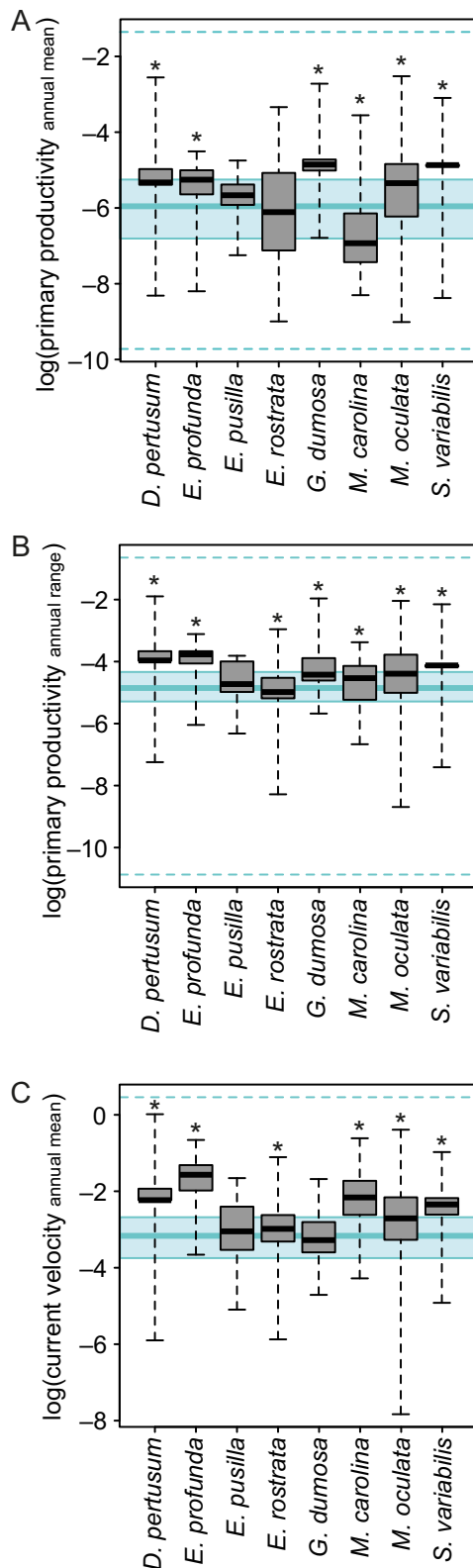
productivity compared to global values (Figs 3B and 5A). A preference for sites with enhanced primary production does not correlate with species-specific differences in depth range (Table 1). Overall, the corals tolerate a broad range of annual primary productivity (Table 3). Secondly, six out of eight reef-forming CWC species occur in areas with above global-average current velocity (Figs 3D and 5C, Table 3). According to our analysis, reef-forming CWCs occur under current velocities of $0.11 \pm 0.07 \text{ m s}^{-1}$ (mean \pm SD; Table 3). With their large, three-dimensional, branching skeletal framework, the corals locally reduce current velocities and create niches with optimal flow for their prey capture (Hennige *et al.*, 2021; Sanna, B scher & Freiwald, 2023), i.e. 0.05 m s^{-1} for phytoplankton (phytodetritus) capture and 0.02 m s^{-1} for zooplankton capture (Purser *et al.*, 2010; Orejas *et al.*, 2016). Currents further drive CWC distribution as they facilitate specific hydrodynamic processes, which spatially and temporally increase the food supply (see Section II.2).

In summary, food supply is an important driver of CWC reef distribution and the combination of enhanced current velocity and increased primary production (among other environmental drivers) can act as powerful predictors of CWC reef presence. However, food supply on and around CWC reefs varies at small spatial and temporal scales, as reviewed below. Accordingly, attempts to predict CWC reef distribution are more or less limited by the resolution of environmental data and the lack of true coral-absence data, due to the high logistic effort and associated costs of surveys (Davies *et al.*, 2008; Georgian, Morgan & Wagner, 2021). In the future, increasing resolution of environmental data, especially of less-common parameters such as POM flux, high-resolution hydrodynamic models and an increasing number of benthic deep-sea surveys globally (Ramirez-Llodra *et al.*, 2010) will likely improve our ability to predict CWC reef occurrences (Rengstorf *et al.*, 2014).

(2) Food pulses created by hydrodynamic processes

Instead of a constantly low food supply, CWCs live in a dynamic environment, where hydrodynamic processes create periodic food pulses at different temporal scales, from a few hours for processes linked to internal tidal activity (e.g. Davies *et al.*, 2009; Duineveld *et al.*, 2012; De Froe *et al.*, 2022), to seasonal cycles (e.g. Mienis *et al.*, 2009; Navas *et al.*, 2014; van der Kaaden *et al.*, 2021) and multiyear cycles such as decadal oscillations (e.g. Guihen, White & Lund lv, 2012; Kazanidis *et al.*, 2021b; Raddatz *et al.*, 2022) and millennial-scale oscillations (Portilho-Ramos *et al.*, 2022). Currents interact with the seafloor, especially with elevated seafloor structures such as oceanic banks [e.g. Galicia Bank and Rockall Bank in the North Atlantic (Duineveld *et al.*, 2004, 2007; White *et al.*, 2005)], continental margins [e.g. the shelf edges of the Faroe islands and Norway (Frederiksen, Jensen & Westerberg, 1992; Thiem *et al.*, 2006)], seamounts (globally, reviewed by White *et al.*, 2007), and fjord sills [e.g. in Norway (R ggeberg

et al., 2011; Wagner *et al.*, 2011)]. Similar current–seafloor interactions are caused by large CWC mounds themselves, e.g. in the Logachev mound CWC province at the slope of



Rockall Bank (Mienis *et al.*, 2007; Cyr *et al.*, 2016; Soetaert *et al.*, 2016; van der Kaaden *et al.*, 2021). These current–topography interactions generate periodic hydrodynamic events like internal tides, trapped waves, and hydraulic jumps (Mohn *et al.*, 2014; van Haren *et al.*, 2014; Cyr *et al.*, 2016). For instance, if an elevated structure partially blocks (tidal) currents, the isopycnals are depressed downstream of this structure, resulting in so-called ‘hydraulic jumps’ (Mohn *et al.*, 2014). Isopycnal depressions and hydraulic jumps accelerate the downward transport of organic matter, from typical particle sinking speeds of a few to hundreds of metres per day (Riley *et al.*, 2012) to vertical transport at 10 cm s^{-1} , corresponding to $>8.5 \text{ km day}^{-1}$ (Davies *et al.*, 2009; Juva *et al.*, 2020). As a result, fresh organic matter is transported from surface waters to CWC reefs in less than 1 h [at the 140 m deep Mingulay reef (Davies *et al.*, 2009; Findlay *et al.*, 2013)]. As the tide reverses, this food pulse moves over the reef and supplies the entire reef community (Davies *et al.*, 2009). Accordingly, fresh, lipid-rich (high-quality) suspended POM has been documented in the bottom water above several CWC reefs/mounds in the North Atlantic (Kiriakoulakis *et al.*, 2007; Mienis *et al.*, 2007; Davies *et al.*, 2009; De Froe *et al.*, 2022). Enhanced concentrations of fresh POM can occur in diurnal or semi-diurnal pulses, linked to the site-specific internal tidal cycle (Duineveld *et al.*, 2007; Mienis *et al.*, 2007; Davies *et al.*, 2009; De Froe *et al.*, 2022). The downward transport of surface organic matter is most pronounced on or close to the reef crest or mound summit (Cyr *et al.*, 2016); accordingly, live CWCs are most abundant here (De Haas *et al.*, 2009; Lim, Wheeler & Arnaubec, 2017; Conti, Lim & Wheeler, 2019; Maier *et al.*, 2021). The fact that large CWC mounds can induce a downward transport of surface organic matter with their own structure (Mienis *et al.*, 2007; Mohn *et al.*, 2014; Soetaert *et al.*, 2016) represents a positive feedback of these mounds on coral growth (van der Kaaden *et al.*, 2020), a remarkable form of ecosystem engineering (*sensu* Jones, Lawton & Shachak, 1994).

Next to accelerating vertical particle transport, tidal currents and internal waves resuspend deposited organic material into bottom or intermediate nepheloid layers, providing another temporal food source for the reefs (Frederiksen *et al.*, 1992; White *et al.*, 2005; Mienis *et al.*, 2007). Besides tidally induced vertical transport, Ekman drainage was proposed as yet another mechanism

Fig. 5. Primary productivity (A: annual mean, B: annual range) and annual mean current velocity (C) at sites with cold-water corals (in grey) in comparison to global values (in blue). Note log-transformed values; for original data and units see Fig. 3 and Table 3. Boxes of boxplots indicate median, first and third quartiles, dotted lines show minimum and maximum values without outliers. Asterisks indicate significant differences between coral sites and global values [$P < 0.05$; Kruskal–Wallis rank-sum tests with *post hoc* Dunn tests; R package FSA (Ogle *et al.*, 2018); for detailed statistical results, see Appendix S2.

Table 3. Primary productivity (annual average and annual seasonal range) and current velocity (annual average) at sites with cold-water corals (CWCs) compared to the global mean. Coordinates of CWC sites were obtained from OBIS (2022), environmental parameters at CWC sites were provided by Bio-ORACLE (Tyberghein *et al.*, 2012; Assis *et al.*, 2018), as described in Appendix S1. For CWCs, values are given separately for the indicated CWC species and pooled for all species (CWCs pooled). Temperatures in CWC habitats are additionally compared to the range of temperatures on tropical coral reefs (Freiwald *et al.*, 2004) because temperature influences physiological processes (Dodds *et al.*, 2007). All given values are model estimates, given at a resolution of 5 arcmin (*ca.* 9.2 km equatorial), not accounting for small-scale variability.

Parameter	Mean \pm SD at locations with CWCs	Global mean \pm SD
Primary productivity: annual average (mg m ⁻³ day ⁻¹)	CWC pooled <i>D. pertusum</i> 8 \pm 10 <i>E. profunda</i> 5 \pm 2 <i>E. pusilla</i> 4 \pm 2 <i>E. rostrata</i> 4 \pm 4 <i>G. dumosa</i> 9 \pm 5 <i>M. carolina</i> 2 \pm 3 <i>M. oculata</i> 6 \pm 8 <i>S. variabilis</i> 8 \pm 2	4 \pm 5
Primary productivity: annual range (mg m ⁻³ day ⁻¹)	CWC pooled <i>D. pertusum</i> 24 \pm 14 <i>E. profunda</i> 21 \pm 9 <i>E. pusilla</i> 11 \pm 7 <i>E. rostrata</i> 8 \pm 6 <i>G. dumosa</i> 17 \pm 12 <i>M. carolina</i> 11 \pm 7 <i>M. oculata</i> 16 \pm 15 <i>S. variabilis</i> 16 \pm 7	11 \pm 12
Current velocity: annual average (m s ⁻¹)	CWC pooled <i>D. pertusum</i> 0.13 \pm 0.08 <i>E. profunda</i> 0.21 \pm 0.09 <i>E. pusilla</i> 0.06 \pm 0.06 <i>E. rostrata</i> 0.06 \pm 0.03 <i>G. dumosa</i> 0.05 \pm 0.03 <i>M. carolina</i> 0.14 \pm 0.1 <i>M. oculata</i> 0.09 \pm 0.09 <i>S. variabilis</i> 0.09 \pm 0.03	0.05 \pm 0.04
Temperature: annual average (°C)	CWC pooled <i>D. pertusum</i> 6.5 \pm 2.4 <i>E. profunda</i> 8.5 \pm 2 <i>E. pusilla</i> 6.1 \pm 3.3 <i>E. rostrata</i> 2.5 \pm 1.8 <i>G. dumosa</i> 6.4 \pm 2 <i>M. carolina</i> 13.5 \pm 6.8 <i>M. oculata</i> 6.2 \pm 3.7 <i>S. variabilis</i> 2.7 \pm 1.3	Global: 1.7 \pm 4.1; tropical coral reefs: 20–29 °C

of food supply to CWC reefs at shelf break regions in the North Atlantic (White *et al.*, 2005; Thiem *et al.*, 2006; Simpson & McCandliss, 2013). Here, an along-slope surface

current is deflected at depth, at an angle of 90°, due to the Coriolis force (Ekman, 1905). As a result, organic matter-rich bottom water from shallower areas above the continental shelf is transported downwards across the slope at velocities of *ca.* 2 cm s⁻¹ (White *et al.*, 2005; Thiem *et al.*, 2006; Simpson & McCandliss, 2013). Due to lower velocities and longer distances cross-slope, particle transport from shallow to deep water by Ekman drainage is slower compared to tidally induced processes, but faster than passive settling (White *et al.*, 2005; Davies *et al.*, 2009; Riley *et al.*, 2012; Juva *et al.*, 2020).

In summary, depending on the prevailing hydrodynamic regime, food availability on CWC reefs can change drastically within a couple of hours, creating a ‘feast–famine’ environment. The relative contribution of different hydrodynamic regimes to food supply is likely reef/region-specific, but this remains to be studied.

(3) Seasonal variability of food pulses

Most reef-forming CWC species (six out of eight) occur in areas where primary productivity shows higher than average annual variation (Figs 3C and 5B, Table 3, Appendix S2). In temperate regions, such as the North Atlantic and the South Pacific, the seasonal cycle of light, temperature and nutrient replenishment gives rise to a pronounced spring phytoplankton bloom, followed by a peak in zooplankton abundance (Lalli & Parsons, 1997). In the Gulf of Mexico, seasonal upwelling, variations of mixed layer depth and riverine nutrient discharge cause a strong variation in primary productivity (Müller-Karger *et al.*, 1991; Zavala-Hidalgo *et al.*, 2006). Seasonal variations in upwelling are also responsible for primary productivity fluctuations on the Mauritanian continental margin (Eisele *et al.*, 2011) and in the North East Pacific California Current System (Gruber *et al.*, 2012; Gómez *et al.*, 2018). Periodic peaks of surface primary production create important food peaks for deep-sea benthos (Billett *et al.*, 1983). During the seasonal phytoplankton bloom, POC flux, POC concentration and zooplankton abundance on Tisler reef (North East Skagerrak, depth <200 m) and Nakken reef (Norwegian fjord, depth 200 m) increase by a factor of two or more (Lavaleye *et al.*, 2009; Maier *et al.*, 2020a). Similarly, one/several annual peaks of fluorescence (*ca.* 30% increase) above the CWC reefs in the Cape Lookout area (NW Atlantic) and the Gulf of Mexico indicate seasonal pulses of fresh organic matter (Mienis *et al.*, 2012, 2014). In between the seasonal food peaks, the availability of phytodetritus on the reefs is low (Duineveld *et al.*, 2004, 2007; Mienis *et al.*, 2012, 2014; van Engeland *et al.*, 2019). Alternative resources may then be available, e.g. resuspended, more degraded organic matter (Mienis *et al.*, 2009; Maier *et al.*, 2020a; van der Kaaden *et al.*, 2021), bacterioplankton, and dissolved organic matter (DOM) (Wild *et al.*, 2008, 2009).

Today we know that daily, seasonal, annual, and decadal cycles of primary production shape deep-sea ecosystems, just like in shallow waters. However, the study of ‘deep-sea seasonality’ remains difficult, especially in temperate and sub-

polar areas, due to their difficult year-round accessibility. Hence, seasonal C fluxes to CWC reefs have only been measured on few reefs, mostly in the North Atlantic, and future studies should direct efforts to other CWC reefs worldwide.

(4) The role of live zooplankton

Vertically migrating zooplankton export substantial amounts of C, especially lipids, from the ocean surface to the deep sea (Jónasdóttir *et al.*, 2015; Kiko *et al.*, 2017; Bandara *et al.*, 2021). Most zooplankton spend the night in surface waters, grazing on phytoplankton, and descend to deeper waters (>300 m) at dawn to escape visual predators (Zaret & Suffern, 1976). When passing CWC reefs, they could create important, lipid-rich food pulses for the corals. Vertically migrating zooplankton were observed on CWC reefs over a large depth range, including the relatively shallow Tisler reef (Skagerrak, Norway, <200 m depth; Guihen, White & Lundälv, 2018), Hola reef (Norwegian continental shelf, 260 m depth; van Engeland *et al.*, 2019), and Mingulay reef (Outer Hebrides, 150 m depth; Duineveld *et al.*, 2007), and deeper reefs in the Santa Maria di Leuca CWC Province (Mediterranean, 300–1100 m depth; Carlier *et al.*, 2009), on the Campeche mounds and in the Viosca Knoll area [Gulf of Mexico, *ca.* 500 m (Mienis *et al.*, 2012; Hebbeln *et al.*, 2014)]. Zooplankton are typically also abundant on and above seamounts, sustaining high CWC abundance (Rogers, 1994; Duineveld *et al.*, 2004; Rowden *et al.*, 2010). By contrast, the large CWC reefs on the slope of Rockall Bank (North-East Atlantic, 800 m depth) showed a low zooplankton abundance (Duineveld *et al.*, 2007; De Froe *et al.*, 2022).

Site-specific differences in zooplankton abundance in the deep sea relate to patterns of primary productivity (Hernández-León *et al.*, 2020). Furthermore, local zooplankton populations have specific depth ranges, varying from 300 to 600 m, e.g. at the Bermuda-Atlantic-Time-Series station (Sargasso Sea; Steinberg *et al.*, 2000), to >1000 m depth, e.g. in the Gulf of Mexico (Ochoa *et al.*, 2013; Ursella *et al.*, 2021). Finally, zooplankton overwinter at depth in specific areas like the Norwegian Sea at *ca.* 600 m depth, whereas other areas like the deep Rockall Trough or shallower Norwegian fjords show low zooplankton abundance in winter (Heath *et al.*, 2000; Campbell & Dower, 2003; Maier *et al.*, 2020a). Corresponding to variations in abundance, the importance of live zooplankton in the CWC diet varies among reefs (Duineveld *et al.*, 2004, 2007; Carlier *et al.*, 2009; van Oevelen *et al.*, 2018) and seasons (Maier *et al.*, 2020a). However, most information on zooplankton food for CWCs originates from the North Atlantic, and future research is required to reveal global patterns.

In conclusion, CWC reefs occur in a highly dynamic ‘feast–famine’ environment, where food availability changes substantially, depending on the season, the prevailing hydrodynamic regime, and presence of vertically migrating zooplankton. During feast conditions, food supply likely sustains reef C demand. For instance, during the productive

season, POC fluxes of 3–67 mmol C m⁻² day⁻¹ were measured by sediment traps (Duineveld *et al.*, 2004; Lavaley *et al.*, 2009; Mienis *et al.*, 2012; Khripounoff *et al.*, 2014), which is in the same order of magnitude as the reef C turnover of 11–123 mmol C m⁻² day⁻¹ (4–45 mol C m⁻² year⁻¹, Fig. 4B). It should be noted that sediment traps tend to underestimate POC fluxes, especially when they tilt under high currents (Khripounoff *et al.*, 2014). Furthermore, additional input of zooplankton and/or dissolved organic carbon (DOC), which are not measured by sediment traps, may fill the remaining gap. More precise reef C budgets, however, require C flux data at higher temporal and spatial resolution and the inclusion of C fluxes through zooplankton and DOC. The comparatively low food supply to the reefs in ‘famine’ periods (Duineveld *et al.*, 2004, 2007; Mienis *et al.*, 2012, 2014; van Engeland *et al.*, 2019) is reflected in the large annual C mismatch (Fig. 4B) and suggests that other physiological and ecological mechanisms are at play, as outlined in the following sections.

III. ADAPTATIONS OF COLD-WATER CORALS TO THE FEAST–FAMINE ENVIRONMENT

As established in Section II, CWCs live in a feast–famine environment with strong temporal fluctuations in resource availability and hydrodynamic conditions. At the same time, CWCs have a high C demand, as illustrated by the following simplified annual C budget for *Desmophyllum pertusum* (Fig. 6), the best-studied scleractinian CWC species. Respiration rates of *D. pertusum*, measured by *ex situ* and *in situ* incubations, range between 1.1 and 2.8 mmol C (g coral dry mass) year⁻¹, if CO₂:O₂ = 1 (see Section I; Larsson *et al.*, 2013b; Larsson, Lundälv & van Oevelen, 2013a; Khripounoff *et al.*, 2014; Maier *et al.*, 2019, 2020a; Baussant *et al.*, 2022). C flux (‘loss’) associated with mucus release has been assessed in fewer studies by *ex situ* incubations (Maier *et al.*, 2011, 2016; Naumann, Orejas & Ferrier-Pagès, 2014; Maier *et al.*, 2019) and amounts to 0.2 mmol POC (g coral dry mass)⁻¹ year⁻¹ (Maier *et al.*, 2019; other studies used different units, see Appendix S3). Together, the C demand of *D. pertusum* amounts to 1.3–3.0 mmol C (g dry mass)⁻¹ year⁻¹ (Fig. 6, Appendix S3); similar C budgets for other CWC species remain to be investigated. Additional energetic costs incur for reproduction, but these are less well established: it is known that *D. pertusum*, *E. rostrata*, *G. dumosa*, and *S. variabilis* release a large number of small eggs and sperm (i.e. ‘organic C’) once per year (broadcast spawning), while *M. oculata* produces several smaller cohorts of larger eggs and sperm (Burgess & Babcock, 2005; Waller & Tyler, 2005). The related C expenditure is difficult to assess, but *D. pertusum* showed a 50% lower organic C content after than before the spawning season (January–March in Norway; Brooke & Järnegren, 2013). This difference of 1.5 mmol C (g dry mass)⁻¹ may correspond to the amount of spawned C and suggests a relatively high reproductive

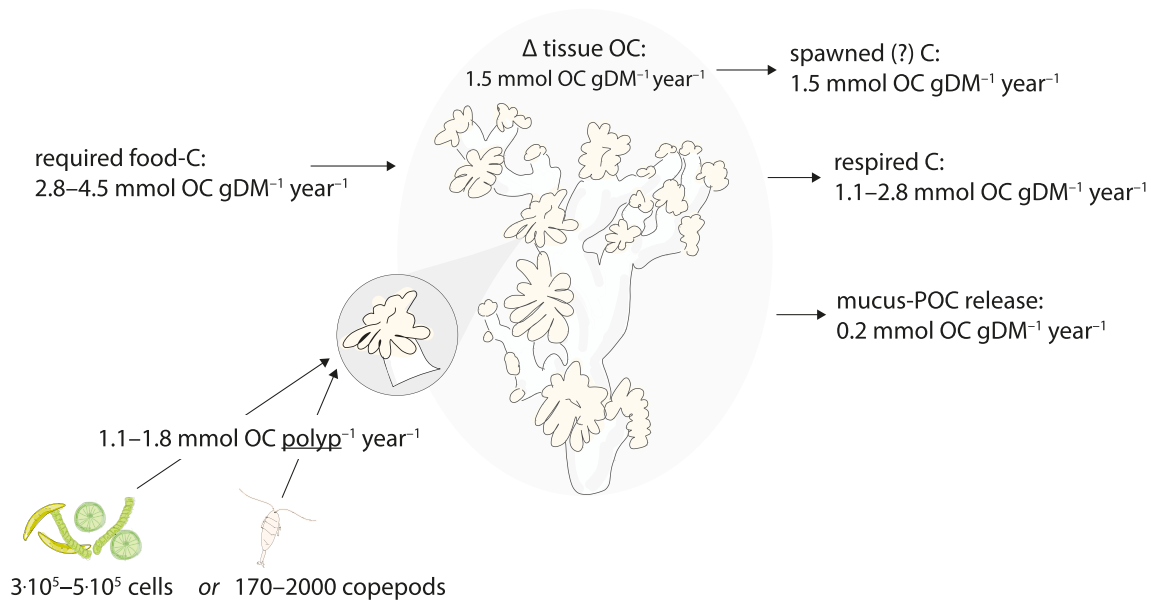


Fig. 6. A simplified annual carbon budget for the cold-water coral *Desmophyllum pertusum*, showing C expenses (right side), leading to estimations of C demand (left side) and corresponding food requirement (phytoplankton, zooplankton). For explanation, references, and calculations see Section III and Appendix S3. DM, dry mass; OC, organic carbon.

cost (Maier *et al.*, 2020a). In total, the annual C budget of *D. pertusum* (Fig. 6) ranges from 2.8 to 4.5 mmol C (g dry mass)⁻¹ year⁻¹, or 1.1 to 1.8 mmol C polyp⁻¹ year⁻¹ (for an average-sized *D. pertusum* polyp of 0.4 g dry mass; Maier *et al.*, 2019). To maintain this C budget, each polyp has to capture *ca.* 170–2000 copepods per year [one copepod ~0.9 to 6.5 μmol C (Grønvik & Hopkins, 1984; Orejas *et al.*, 2016; Höfer *et al.*, 2018)] or 3×10^5 to 5×10^5 live phytoplankton cells per year [one phytoplankton cell ~0.003 μmol C (Orejas *et al.*, 2016)]; for calculations, see Appendix S3.

CWCs seem to meet large parts of their annual C demand by efficiently exploiting large food pulses. As passive suspension feeders, CWCs rely on water flow for their food supply (Gili & Coma, 1998). The corals are optimally adapted to site-specific hydrodynamic conditions and food availability, through variable colony morphology among and within species (De Clippele *et al.*, 2017b; Vad *et al.*, 2017; Hennige *et al.*, 2021; Sanna & Freiwald, 2021; Sanna *et al.*, 2023). For example, fan-shaped colonies (*M. carolina*, *E. rostrata*) often grow perpendicular to unidirectional currents, optimising prey capture (Fricke & Meischner, 1985). *D. pertusum* adapts its morphology based on the prevailing hydrodynamic conditions (Sanna *et al.*, 2023), forming bush-like colonies with more compact upstream branches under higher, unidirectional flow velocities and symmetrical cauliflower-shaped colonies with thinner, ramified branches under more sheltered conditions with lower, multidirectional flow (De Clippele *et al.*, 2017b). These adaptations create efficient suspension feeders. At concentrations of 100 copepods l⁻¹, *D. pertusum* can catch around 12–23 copepods polyp⁻¹ h⁻¹, depending on the flow speed (Orejas *et al.*, 2016; highest

capture at 2 cm s⁻¹, lowest at 10 cm s⁻¹). This corresponds to a C uptake of 11–150 μmol C polyp⁻¹ h⁻¹ (using the copepod C content range mentioned above; Appendix S3). Prey capture rates increase further with increasing zooplankton concentration (Purser *et al.*, 2010). The smaller polyps of *M. oculata* show lower capture rates of large zooplankton compared to *D. pertusum*, but on the scale of a coral colony, this effect is outweighed by the higher polyp density (Tsounis *et al.*, 2010). At high phytoplankton concentrations, as may occur during rapid downwelling events in the productive season (Davies *et al.*, 2009), *D. pertusum* is able to retain up to 6×10^4 phytoplankton cells polyp⁻¹ h⁻¹, i.e. *ca.* 200 μmol C polyp⁻¹ h⁻¹ (Orejas *et al.*, 2016). Hence, during such zooplankton or phytoplankton food pulses, the corals might be able to sustain 1–17% of their annual C demand in only 1 hour (for calculation, see Appendix S3). *In situ* data confirm the potential of CWCs to exploit food pulses and their energetic value: on the Norwegian shelf, *D. pertusum* changes its polyp (feeding) activity in accordance with diurnal changes in current speed and direction, which likely cause periodic changes in food availability (Buhl-Mortensen, Tenningen & Tysseland, 2015; Osterloff *et al.*, 2019). On Nakken reef (Norwegian fjord), *D. pertusum* doubled its organic C content or biomass during the annual spring bloom (Maier *et al.*, 2020a), showing the importance of seasonal food pulses for the annual C budget of these corals.

CWCs store excess assimilated resources from food pulses or periods of high food availability as tissue reserves (Maier *et al.*, 2019). To store reserves, CWCs contain a substantial amount of neutral lipids, i.e. triacylglycerols for short-term storage and wax esters for long-term storage (Dodds *et al.*, 2009; Larsson *et al.*, 2013a; Galand *et al.*, 2020). The

build-up of lipid reserves depends on the CWC species and diet. Experiments showed that *D. pertusum* prefers a zooplankton diet to build-up storage lipids (Galand *et al.*, 2020). *In situ* (Norway), this species formed lipid reserves after the zooplankton bloom in summer, while the earlier spring phytoplankton bloom (phytodetritus peak) was mostly invested in proteins (Maier *et al.*, 2020a). By contrast, *M. oculata* benefits more from a phytodetritus or mixed phytodetritus–zooplankton diet to build up lipid stores (Galand *et al.*, 2020).

The original hypothesis that CWCs draw on their lipid reserves in food-limited periods was, however, not confirmed for *D. pertusum*. When experimentally starved, the corals showed either no decline in storage lipids (Baussant *et al.*, 2017), or a decline in storage lipids that was independent of their feeding status (high *versus* low food; Larsson *et al.*, 2013a). In temperate areas, the lipid content of *D. pertusum* did not decrease steadily over winter (Dodds *et al.*, 2009). Nevertheless, the species did show a seasonal cycle of build-up and decline in lipids closely related to its gametogenesis and spawning. Lipid reserves were formed during summer, in the period of highest oocyte growth, maintained until late winter (December), following which >50% were released between December and February, presumably during a mass-spawning event (Brooke & Järnegren, 2013; Maier *et al.*, 2020a). Hence, CWCs seem to use their lipid reserves rather to sustain their high reproductive costs than to overcome low-food periods. It appears likely that food availability governs the reproductive timing of broadcast-spawning CWCs for two reasons. Firstly, synchronising cost-intensive spawning with the approaching spring bloom allows the resource-depleted adult coral colonies to restock (Maier *et al.*, 2020a). Secondly, the coral larvae start feeding at 3 weeks of age and might profit from abundant phytoplankton (Strömberg & Larsson, 2017). Increased food availability may also trigger periodic spawners (e.g. *M. oculata*) to produce and spawn gametes several times a year (Waller & Tyler, 2005).

Conservation of tissue reserves, in spite of low food availability (e.g. in winter), could be facilitated by a switch to alternative resources. For example in the Rockall Bank area, increased internal wave activity in winter resuspends sediment and resupplies the CWC reefs with more degraded organic particles (Mienis *et al.*, 2009; van der Kaaden *et al.*, 2021), which could, in turn, release DOM and attract bacterioplankton. Feeding experiments demonstrated that CWCs are able to consume these alternative resources, i.e. bacterioplankton, detritus (*D. pertusum*; Mueller *et al.*, 2014) and DOM [*D. pertusum*, *M. oculata* (Gori *et al.*, 2014; Mueller *et al.*, 2014)]. Their close association with a species-specific microbiome (Hansson *et al.*, 2009; Schöttner *et al.*, 2012) further allows *D. pertusum* to feed on inorganic resources, such as inorganic C (coupled to nitrification), dinitrogen and ammonium. However, these chemoautotrophic pathways only contributed 2% to their respiratory C demand (Middelburg *et al.*, 2015). Two studies underline consumption of alternative resources *in situ*. Firstly, the occurrence of *E. rostrata* and *M. oculata* in the New Zealand region is

driven by DOM concentration (Tracey *et al.*, 2011). Secondly, *D. pertusum* in a Norwegian fjord switched from a zooplankton–phytodetritus diet to more degraded material/bacteria in winter, indicated by decreased $\delta^{13}\text{C}$ and increased bacteria fatty acid trophic markers (Maier *et al.*, 2020a). Other studies, however, indicate that *M. oculata* is a less-opportunistic feeder than *D. pertusum* (Galand *et al.*, 2020) and therefore less adapted to variations in resource supply (Chapron *et al.*, 2020). Future research should address variability in resource flexibility among CWC species.

Finally, CWCs may also conserve tissue reserves and energy through low metabolic activity and growth. Facilitated by lower temperatures (Table 3), the respiration rate of CWCs is almost 60% lower compared to their tropical zooxanthellate relatives (Naumann *et al.*, 2011). Correspondingly, CWCs grow about 10 times slower compared to their tropical, shallow-water relatives, i.e. at rates between 0.02% mass increase per day (*D. pertusum*) and 0.2% per day (*M. oculata*) (Orejas *et al.*, 2011a,b). Nevertheless, growth rates vary considerably depending on the local environmental conditions and can reach up to 4 cm year⁻¹, rates comparable to some shallow-water corals (Chapron *et al.*, 2020). While low metabolism and growth may represent general adaptations of CWCs, their reaction to seasonal food shortage differs among species. Under long-term (7-month) experimental food deprivation, *D. pertusum* slowly reduced its metabolic rate by 40–50% in total, but maintained skeletal growth rates (Larsson *et al.*, 2013a; Baussant *et al.*, 2017). By contrast, its close relative *Desmophyllum dianthus* (a non-reef-building, solitary CWC) immediately and strongly reduced skeletal growth and metabolic rate in response to short-term experimental food deprivation (Naumann *et al.*, 2011). *In situ*, *D. pertusum* maintained skeletal growth and budding in seasons with reduced food supply (Lartaud *et al.*, 2014; Maier *et al.*, 2020a). However, increased metabolic rates and decreased skeletal growth during the period of highest oocyte growth suggested an energetic trade-off between reproduction and skeletal growth (Maier *et al.*, 2020a). *M. oculata* (Mediterranean) showed more pronounced seasonal differences in budding (reduced in summer) and skeletal growth (reduced in winter/spring) compared to *D. pertusum*, possibly related to its periodic reproduction or a lower dietary flexibility (Lartaud *et al.*, 2014). *M. oculata* may be more sensitive to varying food availability than *D. pertusum* (Lartaud *et al.*, 2014; Chapron *et al.*, 2020). Species-specific differences in CWC C budgets and adaptations to low-food periods may explain differences in distribution and resilience; hence, future research efforts should aim at including a broader range of different CWC species.

Interannual growth patterns also relate to fluctuating food supply. In the NW Mediterranean, *D. pertusum* and *M. oculata* grew faster (polyp budding and/or linear growth) in years with higher seasonal downwelling intensity caused by episodic dense shelf water events (Chapron *et al.*, 2020). Furthermore, in years with higher sedimentation, the CWCs grew slower, related to less-efficient feeding and energetic costs of

sediment cleaning; in years with particularly strong currents, the corals formed thicker colonies and allocated energy to polyp budding over linear growth (Chapron *et al.*, 2020).

In summary, *D. pertusum* is well adapted to the feast–famine environment through its high physiological flexibility: (i) phytodetritus and zooplankton food pulses are effectively exploited, but when absent, the corals switch to alternative resources; (ii) growth rates are low, but can be boosted during high food availability; (iii) build-up and expenditure of tissue reserves, mostly for reproduction, are synchronised with the seasonal changes in resource supply. Additional work is needed on the physiological flexibility of other CWC species. By contrast, the accumulated knowledge on *D. pertusum* provides the chance to move from simple C budgets (Fig. 6) to more complex dynamic energy budget (DEB) models (Kooijman, 2000; van der Meer, 2006). While rarely applied to deep-sea species due to limited data availability, DEB theory provides a useful model framework to understand, for example, how species can grow (in size, tissue reserves) and reproduce under varying food availability in the deep sea (Gaudron, Lefebvre & Marques, 2021).

IV. HOW DO COLD-WATER CORAL REEFS SUSTAIN THEIR HIGH FOOD DEMAND?

Reef-building CWCs may be well adapted to their ‘feast–famine’ environment, yet, the entire CWC reef community, i.e. the corals and reef-associated fauna and microbes require more food to sustain their high biomass and metabolic activity than they receive in terms of deposited particulate organic matter (see Section I). Based on the literature reviewed here, we suggest two interdependent mechanisms that may explain this mismatch in the reef (organic) C budget: (i) the reef acts as a mechanical and biological filter for phytodetritus (POM); and (ii) recycling (re-use) of C and N within the reef community limits material loss.

(1) The reef filter

A CWC reef represents a giant filter composed of different filter mechanisms (mechanical and biological) and mesh sizes (Fig. 7; Lavaleye *et al.*, 2009; Soetaert *et al.*, 2016; Maier *et al.*, 2021). The reef framework (Fig. 2) acts as mechanical filter (Fig. 7) that baffles the flow and increases the deposition of phytodetritus particles (POM; Dorschel *et al.*, 2005; Mienis *et al.*, 2019). Accordingly, organic matter concentration in the sediment below the reef framework is higher than in sediment off-reef (De Froe *et al.*, 2019). Deeper sediment layers below CWC reefs, however, show extremely low rates of anaerobic C mineralisation, because most organic matter is consumed and mineralised in the overlying ‘reef filter’ (Wehrmann *et al.*, 2009). In addition, suspension-feeding epifauna are highly abundant on CWC reefs (Mortensen & Fosså, 2006; Henry & Roberts, 2007) and create a biological filter for phytodetritus and zooplankton. Reef-forming

CWCs change the environment to optimise (their own) suspension feeding, e.g. by modifying their hydrodynamic environment (Hennige *et al.*, 2021) and by reaching into the upper, current-exposed benthic boundary layer (Buhl-Mortensen *et al.*, 2010). This benefits other suspension-feeding epifauna (Buhl-Mortensen *et al.*, 2010). In a ‘habitat cascade’, different epifauna taxa grow on top of each other [e.g. bryozoans growing on bivalve shells (Kazanidis *et al.*, 2016; Kazanidis, Henry & Roberts, 2021a)] to access fresh phytodetritus (POM; Duineveld *et al.*, 2007). Suspension feeders have evolved a variety of feeding mechanisms (e.g. active *versus* passive) and complex feeding structures specialised on different particle sizes (Gili & Coma, 1998). For example, CWCs capture live zooplankton at high rates (Purser *et al.*, 2010; Orejas *et al.*, 2016) when available (see Section II.4). The large reef bivalve *Acesta excavata* (Fabricius, 1779) shows extraordinarily high clearance rates for phytoplankton or phytodetritus (Järnegren & Altin, 2006), but only limited consumption of smaller-sized bacteria (Maier *et al.*, 2020b). By contrast, sponges such as *Geodia barretti* (Bowerbank, 1858) or *Mycale lingua* (Bowerbank, 1866) retain bacterioplankton with a near 100% efficiency (Pile, Patterson & Witman, 1996; Maier *et al.*, 2020b). Similarly, suspension feeders have a specific hydrographical niche, determined, e.g. by small-scale variations in flow (Henry, Davies & Roberts, 2010). Active suspension feeders are typically more reliant on POM concentration than on POM flux (Lesser, Witman & Sebnens, 1994). Accordingly, some active suspension feeders, e.g. the sponge *Hymedesmia paupertas* (Bowerbank, 1866), prefer current-sheltered reef sites (Henry *et al.*, 2010). Small-scale spatial segregation (Purser *et al.*, 2013; Robert *et al.*, 2020) may reduce competition where dietary niches overlap (van Oevelen *et al.*, 2018). Acting as a mechanical and biological filter, CWC reefs deplete phytodetritus (POM) from the bottom water (Lavaleye *et al.*, 2009; Wagner *et al.*, 2011).

The branched, porous reef framework brings abundant suspension-feeding epifauna into close contact with detritivores (Mortensen *et al.*, 1995; Henry & Roberts, 2007) and a diverse microbial community (van Bleijswijk *et al.*, 2015), giving rise to a complex food web (van Oevelen *et al.*, 2009). Particles mechanically intercepted by the reef framework serve as a food source for detritivores such as echiuran worms (Kiriakoulakis *et al.*, 2004) or ophiuroids (Maier *et al.*, 2021). The tube-building polychaete *Eunice norvegica* (Linnaeus, 1767) forms a symbiosis with *D. pertusum*: the polychaete benefits from stealing food particles from the coral and at the same time it keeps its host clean from accumulating detritus and stabilises the reef framework by building tubes between the framework branches (Mortensen, 2001; Roberts, 2005; Mueller *et al.*, 2013).

(2) Recycling of metabolic ‘waste’ products

The high organic matter mineralisation on CWC reefs leads to an accumulation of faunal waste products, e.g. detrital

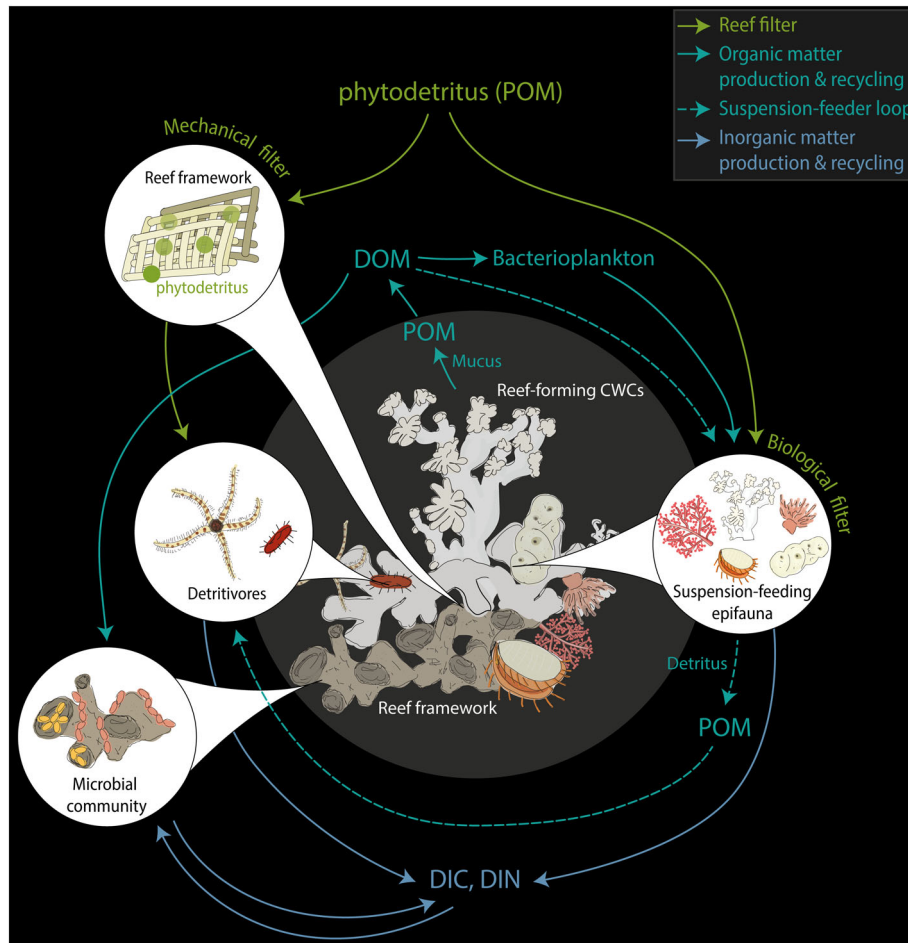


Fig. 7. The cold-water coral (CWC) ‘reef filter’ and recycling of C and N within the reef community. Filtration and subsequent consumption of phytodetritus, a form of particulate organic matter (POM), are shown in green. Production and recycling of organic matter are in turquoise, e.g. coral mucus [POM, dissolving to dissolved organic matter (DOM)], sponge detritus, or bivalve (pseudo-)faeces. Production and recycling of inorganic matter is in light blue, i.e. dissolved inorganic C (DIC) and N (DIN; ammonium recycling for example).

POM, DOM, dissolved inorganic carbon and nitrogen (DIC, DIN) (Wild *et al.*, 2008; Wagner *et al.*, 2011; Khripounoff *et al.*, 2014; De Froe *et al.*, 2019). For instance, CWCs release mucus (Wild *et al.*, 2008), a polysaccharide–protein complex, for protection against biofouling and sedimentation and as a feeding aid (Fig. 7; Bythell & Wild, 2011; Zetsche *et al.*, 2016; Murray *et al.*, 2019). Mucus detaches from the corals (Wild *et al.*, 2004) and enhances the concentration of labile (high-quality) POM downstream of the reef (Wagner *et al.*, 2011). Most of the mucus dissolves rapidly, creating a pool of labile DOM (Wild *et al.*, 2008). Typically limited in deep-sea water (Carlson & Hansell, 2015), coral-derived labile DOM promotes the activity and growth of bacterioplankton (Fig. 7; Wild *et al.*, 2008, 2009). Bacterioplankton, in turn, provide a high-quality substrate for reef sponges, as outlined above (Pile *et al.*, 1996; Leys *et al.*, 2018; Maier *et al.*, 2020b). The recycling of ‘waste DOM’ by bacterioplankton returns material and energy to higher trophic levels (Fig. 7), corresponding to the microbial loop in surface-waters (Azam *et al.*, 1983).

Moreover, suspension feeders can directly consume and recycle DOM (Fig. 7, Table 4). Deep-sea sponges are well-known DOM consumers (Table 4), just like their shallow-water counterparts (reviewed by De Goeij, Lesser & Pawlik, 2017). Initially, symbiotic microbes were considered responsible for the high DOM uptake of sponges (Reiswig, 1981; Yahel *et al.*, 2003; Ribes *et al.*, 2012). Specifically in high-microbial-abundance (HMA) sponges, microorganisms contribute 20–35% to the total sponge biomass (Reiswig, 1981; Hentschel, Usher & Taylor, 2006). Recent research, however, challenged this paradigm: Firstly, low-microbial-abundance (LMA) sponges consume and assimilate DOM at high rates (Table 4; De Goeij *et al.*, 2017), but host microorganisms at concentrations only equivalent to those in the surrounding sea water (Hentschel *et al.*, 2006). Secondly, stable isotope tracer experiments demonstrated direct uptake of DOM by sponge cells (Rix *et al.*, 2020) and incorporation of DOM-derived C into *de novo*-synthesised and/or sponge-specific fatty acids (Rix *et al.*, 2016;

Table 4. Consumption of dissolved organic matter (DOM) by benthic invertebrates from cold-water coral reefs and deep-sea sponge grounds. HMA, high-microbial abundance sponge; LMA, low-microbial abundance sponge. POM, particulate organic matter.

Study	DOM substrate	Species	Phylum, class, (description)
Van Duyl <i>et al.</i> (2008)	³ H-leucine (amino acid)	<i>Higginsia thielei</i> <i>Nodastrella nodastrella</i> (formerly: <i>Rossella nodastrella</i>)	Porifera, Demospongiae (HMA) Porifera, Hexactinellida (massive, HMA)
Gori <i>et al.</i> (2014)	Dissolved free amino acids	<i>Desmophyllum pertusum</i> , <i>Desmophyllum dianthus</i> , <i>Dendrophyllia cornigera</i> , <i>Madrepora oculata</i>	Cnidaria, Anthozoa
Mueller <i>et al.</i> (2014)	¹³ C-dissolved free amino acids	<i>Desmophyllum pertusum</i>	Cnidaria, Anthozoa
Rix <i>et al.</i> (2016)	Coral mucus (POM, DOM)	<i>Hymedesmia coricea</i>	Porifera, Demospongiae (encrusting, LMA)
Kazanidis <i>et al.</i> (2018)	¹³ C-glucose	<i>Spongosorites coralliophaga</i>	Porifera, Demospongiae (massive)
Bart <i>et al.</i> (2020)	¹³ C-DOM (from lysed diatoms)	<i>Geodia barretti</i> <i>Hymedesmia paupertas</i>	Porifera, Demospongiae (massive, HMA) Porifera, Demospongiae (encrusting, LMA)
Maier <i>et al.</i> (2020b)	¹³ C-DOM (from lysed diatoms)	<i>Vazella pourtalesii</i> <i>Geodia barretti</i> <i>Acesta excavata</i>	Porifera, Hexactinellida (massive, LMA) Porifera, Demospongiae (massive, HMA) Mollusca, Bivalvia
Bart <i>et al.</i> (2021b)	Natural DOM	<i>Vazella pourtalesii</i> <i>Geodia barretti</i> <i>Geodia atlantica</i> <i>Acantheurypion spinispinosum</i>	Porifera, Hexactinellidae (LMA; massive) Porifera, Demospongiae (HMA; massive) Porifera, Demospongiae (HMA; massive) Porifera, Demospongiae (LMA; encrusting)
Maier <i>et al.</i> (2021)	¹³ C-DOM (from lysed diatoms)	Porifera Stylasteridae <i>Protanthea simplex</i> Alcyonacea <i>Asperarca nodulosa</i> Pectinidae <i>Lima marioni</i> Ophiuroidea Hesionidae <i>Chaetopterus</i> sp. Polynoidae	Porifera Cnidaria, Hydrozoa Cnidaria, Anthozoa Cnidaria, Anthozoa Mollusca, Bivalvia Mollusca, Bivalvia Mollusca, Bivalvia Echinodermata, Ophiuroidea Annelida, Polychaeta Annelida, Polychaeta Annelida, Polychaeta

Bart *et al.*, 2020). Thirdly, several other suspension-feeding taxa on CWC reefs consume and assimilate DOM, including several scleractinian CWC species (Gori *et al.*, 2014; Mueller *et al.*, 2014), hydrozoans, stylasterid corals, and bivalves (Maier *et al.*, 2020b, 2021). The faunal and microbial community growing on and inside the reef framework meets 30% of its respiratory C demand by uptake of natural DOM (Maier *et al.*, 2021), demonstrating the quantitative importance of this recycling pathway.

In a recycling pathway termed the ‘sponge loop’, sponges recycle substantial amounts of assimilated DOM to particulate ‘sponge detritus’ (POM; Fig. 7), which is consumed by reef detritivores (De Goeij *et al.*, 2013). Originally described for tropical coral reefs (De Goeij *et al.*, 2013), the sponge loop finds an equivalent on CWC reefs (Rix *et al.*, 2016; Bart *et al.*, 2021a). Other suspension feeders, such as bivalves, likewise recycle substantial amounts of DOM to detrital POM, in this case bivalve (pseudo-)faeces, which can be consumed by reef detritivores (Maier *et al.*, 2020b). The prevalence of DOM consumption by reef invertebrates (Table 4) suggests that these ‘suspension feeder’ loops (Fig. 7; Maier

et al., 2020b; Bart *et al.*, 2021a) are ubiquitous within the CWC reef community and future research is likely to reveal more.

Finally, DIC and DIN are recycled by reef microbes that grow on and inside the porous reef framework and as symbionts in invertebrates (Fig. 7). Nitrifying bacteria and archaea associated with the reef framework (van Bleijswijk *et al.*, 2015) subsist on (faunal) ammonium, which they transform to nitrate (nitrification; Maier *et al.*, 2021); thereby gaining energy for chemoautotrophic DIC fixation. Furthermore, HMA sponges and their diverse microbiome (Hentschel *et al.*, 2006) perform a variety of nutrient fluxes together, e.g. aerobic and anaerobic respiration, nitrification of sponge-derived ammonium and coupled DIC fixation, denitrification of nitrate to dinitrogen gas, and anaerobic ammonium oxidation (anammox) (Hoffmann *et al.*, 2009; De Kluijver *et al.*, 2021). Microbially fixed C is transferred to the sponge hosts (van Duyl *et al.*, 2020), e.g. *via* the consumption of microbes *via* phagocytosis (Leys *et al.*, 2018). Mediating diverse internal and external recycling pathways, sponges act on and connect several trophic levels and play

an ubiquitous role in deep-sea ecosystems (Hanz *et al.*, 2022). CWCs also host a microbiome, enabling them to perform similar nutrient fluxes, but these play a minor quantitative role in the total CWC metabolism (Middelburg *et al.*, 2015). Altogether, the microbial community contributes substantially to the total organic matter mineralisation of CWC reefs (van Oevelen *et al.*, 2009; Maier *et al.*, 2021).

In conclusion, the high ecological efficiency of CWC reefs may explain the mismatch in their organic C budget (Fig. 4B). While the 'reef filter' ensures optimal retention of zooplankton, phytodetritus, and bacterioplankton, sediment traps only measure the deposition of phytodetritus (POM). Hence, sediment traps underestimate the actual food retention by CWC reefs, especially under high current velocities (Gardner, Biscaye & Richardson, 1997; Mienis *et al.*, 2009; van Oevelen *et al.*, 2009). Moreover, diverse trophic interactions and material recycling facilitate optimal utilisation of the retained food and exploitation of additional resources beyond deposited POM, such as dissolved organic and inorganic matter. Nevertheless, the quantitative importance of recycling pathways and their link in the reef food web remain vague. Modern mapping attempts of reef biomass and metabolic activity detail the importance of CWC reefs in the regional C cycle (De Clippele *et al.*, 2021a,b). In a logical next step, reef food web (C cycling) models (e.g. van Oevelen *et al.*, 2009) could be updated with recycling pathways to estimate how much of the retained and/or metabolised material is recycled, how filtration and recycling contribute to reef (biomass) growth, and how much metabolic 'waste' material is lost from the reef ecosystem. Another essential question in this context is the importance of (functional) biodiversity for the filtration and recycling capacity of the reef, and hence its biomass, metabolic activity and resilience to changing conditions, which we discuss in the following section.

V. PERSPECTIVES: COLD-WATER CORAL REEFS IN THE ANTHROPOCENE

In the Anthropocene, each of the mechanisms discussed above that sustain CWC reefs in the food-limited deep sea have become threatened. The ocean, including the deep sea, is becoming warmer, less well mixed and more acidic, with pollution, fisheries and mining aggravating global change (Gruber, 2011; Roberts & Cairns, 2014; Sweetman *et al.*, 2017). Anthropogenic environmental change disbalances the energy budget of reef-building corals (Fig. 8A) and destabilises the reef framework, resulting in decreased reef biodiversity and functioning (Fig. 8B).

(1) Disbalanced energy budget of cold-water corals

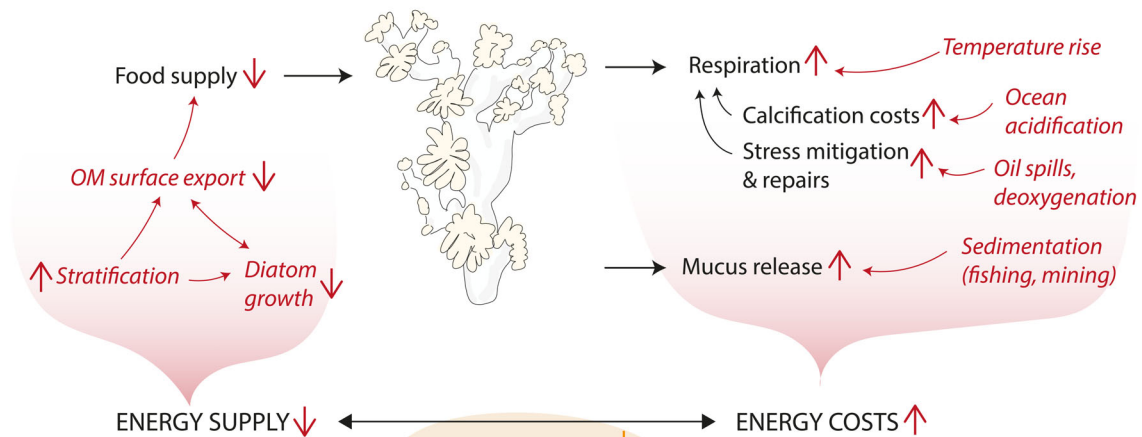
A disbalanced energy budget of CWCs is the result of decreasing food supply on the one hand, and increasing energetic costs on the other (Fig. 8A). As the ocean surface is

warming more rapidly than the rest of the water column, the water column becomes more stratified (Bopp *et al.*, 2001; Gruber, 2011; Capotondi *et al.*, 2012). Enhanced stratification decreases the intensity of the hydrodynamic mixing processes (Bopp *et al.*, 2001; Li *et al.*, 2020) that supply CWC reefs with important food pulses (see Section II.2). In addition, reduced upwelling of nutrient-rich bottom water limits diatom growth, further reducing POM export (Bopp *et al.*, 2005).

At the same time, bottom-water temperature in the bathyal is projected to increase by 3–4 °C by 2100 (Mora *et al.*, 2013; Sweetman *et al.*, 2017). Increasing temperatures spur the corals' respiratory activity and metabolic costs (Dodds *et al.*, 2009; Dorey *et al.*, 2020; Gómez *et al.*, 2022). Initially, CWCs may benefit from higher temperatures, through enhanced polyp activity, higher prey capture rates (Chapron *et al.*, 2021) and growth (Büscher, Form & Riebesell, 2017; Büscher *et al.*, 2022). Nevertheless, beyond a certain temperature threshold (+4 °C), enhanced food intake is no longer sufficient to offset the metabolic energy costs (Chapron *et al.*, 2021) or prey capture decreases, leading to decreased growth, tissue reserves, and eventually death (Gómez *et al.*, 2022). Furthermore, even small changes in temperature affect the CWC microbiome, with potential consequences for microbially assisted nutrient acquisition and immune responses (Chapron *et al.*, 2021).

Moreover, high atmospheric CO₂ concentrations lead to ocean acidification (Kleypas *et al.*, 1999; Wolf-Gladrow *et al.*, 1999) and a projected decrease of 0.3 pH units in the bathyal by 2100 (Sweetman *et al.*, 2017). More acidic conditions render calcification, i.e. the formation of calcium carbonate (aragonite) skeletons, more energetically costly (Cohen & Holcomb, 2009). Due to the naturally low carbonate (aragonite) saturation in their deep, cold habitat, CWCs are particularly vulnerable to ocean acidification (Orr *et al.*, 2005; Guinotte *et al.*, 2006; Lunden, Georgian & Cordes, 2013; Gómez *et al.*, 2018). Nevertheless, CWCs, particularly some genotypes, are able to acclimatise and maintain skeletal growth under long-term exposure to experimental acidification (Form & Riebesell, 2012; Maier *et al.*, 2013; Hennige *et al.*, 2014, 2015; Movilla *et al.*, 2014; Büscher *et al.*, 2017; Kurman *et al.*, 2017; Gammon *et al.*, 2018). The metabolic stimulation by higher temperatures may partially offset the negative impact of acidification on CWC growth up to a certain temperature and pH threshold (Büscher *et al.*, 2022). At several sites, CWCs (*D. pertusum*, *E. rostrata*, *G. dumosa*, *M. oculata*, *S. variabilis*) even grow under aragonite undersaturation (Thresher *et al.*, 2011; Bostock *et al.*, 2015; Baco *et al.*, 2017). To calcify under low pH, corals may upregulate their internal pH through ion transport (McCulloch *et al.*, 2012a,b; Wall *et al.*, 2015; Glazier *et al.*, 2020). The involved energetic cost, however, increases by 10% per 0.1 pH unit decrease in seawater pH (McCulloch *et al.*, 2012b), hence, the ability of CWCs to locally acclimatise or adapt to acidified conditions may depend greatly on the respective food supply (Georgian *et al.*, 2016).

A Energy budget of cold-water corals (CWCs)



B Reef functioning

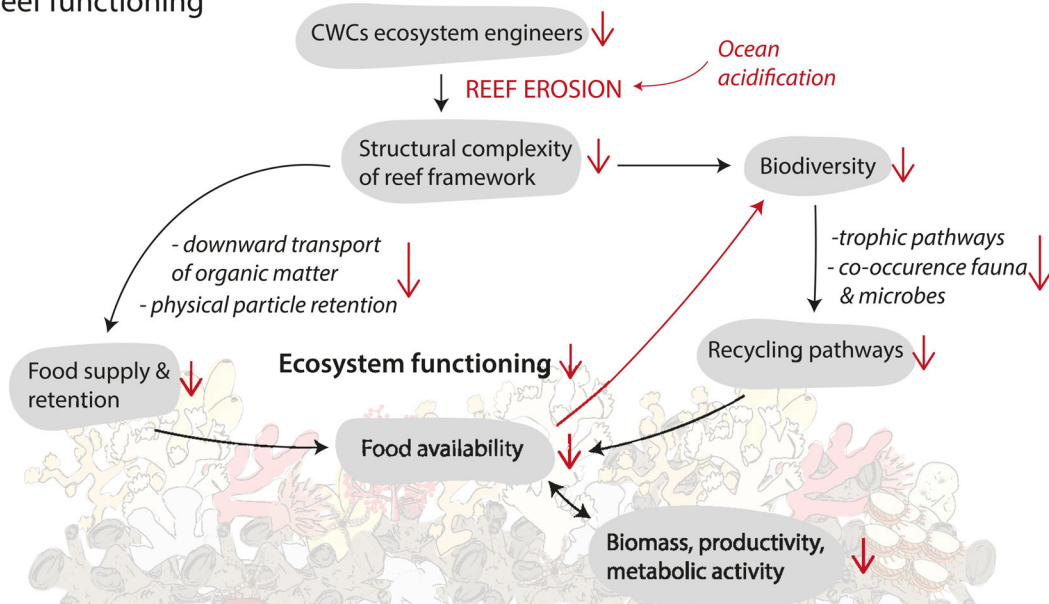


Fig. 8. Negative impacts of anthropogenic environmental change (in red) on (A) the energy budget of cold-water corals (CWCs) and (B) CWC reef ecosystem functioning. OM, organic matter.

Other anthropogenic impacts additionally disbalance the energy budget of CWCs, by increasing their energetic costs to mitigate stress while at the same time decreasing their prey-capture rates (Fig. 8A); these impacts include physical abrasion and increased sedimentation through fisheries and

mineral extraction (Fossa, Mortensen & Furevik, 2002; Davies, Roberts & Hall-Spencer, 2007; Armstrong & van den Hove, 2008; Huvenne *et al.*, 2016), oxygen stress through increasing deoxygenation of bottom waters (Dodds *et al.*, 2007; Sweetman *et al.*, 2017; Hanz *et al.*, 2019;

Hebbeln *et al.*, 2020), and pollution by oil spills (Weinnig *et al.*, 2020) and plastic (Chapron *et al.*, 2018; Mouchi *et al.*, 2019).

In situ, CWCs already show signs of energetic shortfalls. In seasonal periods of enhanced metabolic activity, possibly due to reproductive tissue modifications, *D. pertusum* showed on average *ca.* 70% lower linear skeletal extension rates compared to other seasons (Maier *et al.*, 2020a). Likewise, in years of low downwelling/water-column mixing intensity, the species showed on average *ca.* 80% lower linear skeletal extension rates compared to high-mixing years (Chapron *et al.*, 2020). Furthermore, corals at heavily trawled sites are non-reproductive, possibly because their energy reserves (and colony size) are too low to afford sexual reproduction (Waller & Tyler, 2005). Altogether, global change is predicted to reduce the habitat suitable for CWCs by 79% (Morato *et al.*, 2020) and CWC reef biomass by 38% (Jones *et al.*, 2014) by 2100.

(2) Reduced reef functioning on ‘crumbling’ reefs

On the ecosystem level, decreased coral growth on the one hand, and increased erosion of the reef framework on the other hand (Fig. 8B), threaten the reef carbonate budget (Perry *et al.*, 2013; Büscher *et al.*, 2019). Under low pH, CWC skeletons are more porous and form a less stable reef framework (Hennige *et al.*, 2015). Furthermore, ocean acidification accelerates chemical dissolution and bioerosion of the calcium carbonate reef framework (Wisshak *et al.*, 2012, 2014; Hennige *et al.*, 2015). Altogether, this ‘coralporosis’ produces unstable, ‘crumbling’ reefs of reduced structural complexity, and in case of aragonite undersaturation, CWC ‘reefs’ consisting primarily of live coral colonies without a dead framework foundation (Hennige *et al.*, 2020).

Reduced structural complexity will likely diminish CWC reef biodiversity and ecosystem functioning (Fig. 8B), similar to tropical coral reefs (Nelson, Kuempel & Altieri, 2016; Sunday *et al.*, 2016; Doo, Edmunds & Carpenter, 2019; Dove *et al.*, 2020). A flat reef structure does not induce downward transport of POM-rich surface water, leading to (further) diminished food supply and retention (White *et al.*, 2005; Mienis *et al.*, 2007; Soetaert *et al.*, 2016). Reef sessile suspension feeders cannot attach to strongly degraded reef framework and coral rubble (Mortensen & Fosså, 2006; Maier *et al.*, 2021). Furthermore, suspension feeders appear particularly sensitive to temperature increase, indicated by their reduced abundance under episodic, interannual temperature highs at the Mingulay Reef (Kazanidis *et al.*, 2021b). Loss of structural complexity and suspension feeders on CWC reefs will likely impair the mechanical and biological ‘reef filter’ and concomitantly food particle retention (Fig. 8B; see Section IV). Reduced food availability and decreased biodiversity may restrain recycling pathways. For instance, lower abundance of CWCs could result in lower production of mucoid DOM, less recycling of DOM by the reef fauna, and less production of detrital waste for detritivores – i.e. an attenuated ‘suspension feeder (sponge) loop’

(Fig. 8B). Reduced resource availability might lead to a further decrease of biodiversity (Fig. 8B), creating a detrimental feedback loop that jeopardises the stability of the reef community (Worm & Duffy, 2003). In conclusion, the Anthropocene climate may substantially damage the functioning of CWC reef ecosystems, but unlike for tropical coral reefs (Hughes *et al.*, 2010), virtually nothing is known about their resilience and potential phase shifts. In a similar way, global change will likely affect other complex deep-sea ecosystems, such as coral gardens and sponge grounds (Rossi *et al.*, 2019).

(3) Conservation of cold-water coral reefs in the Anthropocene

The vulnerability of CWC reefs and their importance as ecosystem service providers (see Section I) has been recognised by the United Nations (UN) Food and Agriculture Organisation (FAO, 2009), declaring CWC reefs as vulnerable marine ecosystems (VMEs), according to the United Nations General Assembly (UNGA) resolution 61/105 (UNGA, 2007). VMEs require special protection, e.g. through marine spatial planning with the designation of marine protected areas (MPAs; United Nations, 2017). Yet, effective marine spatial planning remains difficult, due to limited scientific knowledge on global CWC distribution, lack of historical baseline data (Durán Muñoz & Sayago-Gil, 2011; Kazanidis *et al.*, 2020; Lim, Wheeler & Conti, 2021), and scarce data on MPA effectiveness (Huvenne *et al.*, 2016). Some stressors are not constrained by protected area boundaries, including oil, other pollutants and impacts from global change; however protected areas can provide resilience to global stressors by maintaining ecosystem function. Continued mapping and characterisation of CWC habitats is critical, but we argue that our improved understanding of the ‘cold-water coral reef paradox’ should also be incorporated into ecosystem assessment and conservation efforts. Live coral cover has been used as a proxy for CWC reef health (Flögel *et al.*, 2014; Juva *et al.*, 2020), yet differences in CWC cover may be natural and do not necessarily provide information on whether a reef is new or on the verge of disappearing (Hughes *et al.*, 2010). An integrative approach to assess the environmental status of CWC reefs was presented by Kazanidis *et al.* (2020), including biodiversity indices, coral cover, fish biomass, signs of anthropogenic impacts, etc., as proxies for reef status. Based on Sections II–IV, we suggest complementing these ecosystem descriptors by including (i) organic and inorganic C budgets for (a) CWCs and (b) the reef ecosystem, to evaluate reef growth *versus* erosion; and (ii) reef functional diversity and food-web complexity, to judge ecosystem functioning and resilience to changing oceanographic conditions. Future research should create a framework to facilitate the assessment of these ecosystem descriptors. For 1a, the energetic status (energy budget) of CWCs at different reefs should be regularly measured, e.g. their metabolic activity and tissue stores (somatic and reproductive). In addition, these measures could be introduced into DEB models, to assess coral

growth under local and potentially changing environmental conditions (e.g. temperature, food supply). Regarding 1b, video transect annotations of CWC reefs can be combined with predictive modelling to create reef-scale biomass, and organic and inorganic C maps; newly developed machine-learning algorithms will accelerate video annotations in the future (De Clippele *et al.*, 2021a). Regarding 2, future research could develop a functional traits database for reef-associated organisms (e.g. their feeding guild) plus open-source code for simple implementation of food-web models. This would allow evaluation of the trophodynamic resilience of different CWC reefs without strong programming skills. Based on these approaches, future research may help to identify CWC reef 'refugia' that are likely to persist during future global change (Morato *et al.*, 2020). Spatial measures protecting networks of these refugia from, e.g. bottom-trawling fisheries, appear to be our best chance to preserve CWC reefs and their function as diversity-productivity hotspots in the deep sea.

VI. CONCLUSIONS

- (1) Recent major advances allow us to approach the paradox of how CWC reefs sustain high biodiversity, biomass and metabolic activity in the food-limited deep sea. Suggested answers to this paradox reveal key drivers of CWC reef distribution that are required to achieve effective conservation measures.
- (2) Most reef-building CWC species occur in areas of enhanced primary production with high seasonal fluctuations and under elevated current velocity (relative to global averages), indicating that food production and supply are important drivers of CWC reef distribution.
- (3) Food supply on CWC reefs is not constantly low, but highly dynamic. Within a couple of hours, food availability can change from very low to very high, depending on the season, the prevailing hydrodynamic regime, and presence of vertically migrating zooplankton.
- (4) The best-studied reef-forming CWC species *D. pertusum* is well adapted to these extreme temporal fluctuations in food availability, by (i) high capture rates of phytodetritus and zooplankton, (ii) high resource flexibility (DOM, bacterioplankton, inorganic resources), (iii) investing in large tissue reserves for reproduction, and (iv) synchronising activity with (seasonal) fluctuations in food availability.
- (5) On the ecosystem level, CWC reefs sustain high metabolic activity and biomass. They achieve this firstly by efficient retention of phytodetritus, zooplankton and bacterioplankton in the 'reef filter', a combination of a mechanical filter provided by the structurally complex, porous reef framework and a biological filter consisting of diverse, abundant suspension-feeding epifauna. Secondly, diverse trophic interactions and material recycling facilitate optimal resource utilisation and exploitation of additional food sources, such as dissolved organic and inorganic matter.

- (6) Climate change, ocean acidification, fisheries, mining, and pollution impact reef functioning in various ways, e.g. by reducing organic matter supply, increasing the animals' energy demands, and dissolving the carbonate reef framework, thereby decreasing structural and biological diversity and ecosystem functioning. Research has only started to reveal the vast complexity, drivers and functioning of CWC reefs, but it is crucial to continue this path to facilitate knowledge-based habitat management for sustaining these diversity-productivity hotspots in the future ocean.

VII. ACKNOWLEDGEMENTS

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VIII. REFERENCES

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Detailed methods.

Appendix S2. Results of statistical analysis of comparisons of primary productivity annual average and annual range, and current velocity annual average at cold-water coral sites with the global mean.

Appendix S3. Respiration, organic matter release, food demand, and food capture of cold-water corals.

Table S1. Flux of particulate organic carbon (POC_{flux}) measured by sediment trap at the indicated sites, depth and during the indicated time span.

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