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The first IUCN Red List of cold-water corals highlights global declines

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Abstract
The most well-known species-based conservation tool is the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species. The current coverage of species in the Red List is known to under-represent benthic marine species. Cold-water corals (CWCs) are increasingly recognised as key to deep-water biodiversity and integral to protected vulnerable marine ecosystems (VMEs), but no deep-sea coral species were previously included in the Red List. We selected 22 cold-water coral species in the Northeast Atlantic, including 4 reef-forming stony corals and 18 octocorals including sea pens and gorgonians, and completed the first IUCN Red List global assessments for corals inhabiting the deep sea. Most of the species assessed herein are habitat-forming, including those that form coral reefs and marine animal forests such as coral gardens or sea pen fields. We assessed eight species as near threatened, and one species as globally vulnerable: *Desmophyllum pertusum. Some of these species are distributed across an entire ocean basin, but the cumulative damage from human impacts have reduced populations by upwards of 30% from recent baselines*. In addition, three species are listed as data deficient, and the remaining 10 species are assessed as least concern. All assessments in threatened categories were made using Red List criterion A, based on evidence of past population declines, and the main threats in most cases are related to bottom-contact fishing. We also present five case studies that illustrate the application of the Red List criteria to cold-water corals. Despite technological limitations to establishing baseline populations, documented large-scale declines of widespread species clearly demonstrate the magnitude of threats to deep-sea ecosystems and the need for large-scale conservation measures.

Keywords Deep-sea corals · Red List · Conservation · Marine biodiversity · Anthropogenic threats · Ocean acidification · Habitat destruction · Ecosystem management · Species-based conservation · Scleractinia · Octocorallia

Abbreviations

AOO	Area of occupancy
CR	Critically endangered (Red List category)
CWC	Cold-water coral
DD	Data deficient (Red List category)
EN	Endangered (Red List category)
EOO	Extent of occurrence
FAO	UN Food and Agriculture Organisation
GBIF	Global Biodiversity Information Facility
IUCN	International Union for the Conservation of Nature
IINH	Icelandic Institute of Natural History
LC	Least concern (Red List category)
NAFO	Northwest Atlantic Fisheries Organization
NEAFC	Northeast Atlantic Fisheries Commission
NT	Near threatened (Red List category)
OBIS	Ocean Biodiversity Information System
OSPAR	Convention for the Protection of the Marine Environment of the North-East Atlantic
Red List	IUCN Red List of Threatened Species
ROV	Remotely operated vehicle
UNGA	United Nations General Assembly
VME	Vulnerable marine ecosystem
VU	Vulnerable (Red List category)

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Introduction

Coral ecosystems are flagship habitats for global conservation, and the complex structure and biodiversity of coral reefs immediately capture the imagination. Coral reefs have persisted for millions of years but are now threatened by the rapid pace of global warming (Jung et al. 2024; Gutierrez et al. 2024). Cold-water corals are found from tropical to polar regions and from the shallows to the deep sea (Roberts 2009) but often beyond 200 m in depth; therefore, they are often also characterized as deep-sea corals. Corals in deep, dark waters expand our understanding of this group to new ecosystems in a dramatically larger part of the world ocean (Roberts et al. 2006; Foley et al. 2010). Tropical, temperate, and cold-water corals create habitats, breeding grounds, and shelter for numerous marine species, many of which are commercially significant (Costello et al. 2005).

All corals are increasingly threatened by anthropogenic activities that cause direct physical damage as well as climate change-induced ocean warming and acidification. In shallow tropical coral reefs, this is shown most visibly through coral bleaching (Carpenter et al. 2008; Gutierrez et al. 2024). Deep-sea corals lack photosymbionts and are not at risk of bleaching, but those with calcium carbonate skeletons can be vulnerable to decreases in pH (Hennige et al. 2015, 2020), and many deep-sea species are very intolerant to temperature increase (Butt et al. 2022). Depth and technological challenges of deep-sea exploration historically hid cold-water coral (CWC) ecosystems from discovery, but meanwhile, they are still vulnerable to impacts from deep-sea fishing. Scleractinian CWCs were not known to form extensive framework structures until reefs were found off the Norwegian coast in the 1940 s (Dons 1944). Now it is widely known that three-dimensional structures of coral create deep-sea biodiversity hotspots, supporting elevated fish population densities that attract fishing pressure, which can lead to accidental harm to the coral framework (Foley et al. 2010; Jackson et al. 2014). Offshore activities that impact the seabed, such as deep-sea mining, or installation of other infrastructure such as deep-sea cables, pylons for oil and gas extraction, or offshore wind turbines, all not only disrupt the seabed directly but also reshape sediment distribution that can smother wildlife distant from the disturbance site (Ragnarsson et al. 2016).

Deep-sea corals include reef-forming stony corals (Scleractinia), black corals (Antipatharia), octocorals (Octocorallia) including sea pens (Pennatuloidea), soft corals and gorgonians, and the lace corals (Stylasteridae), which are calcifying colonial hydrozoans (Roberts et al. 2006; Roberts 2009). A United Nations (UN) resolution on sustainable fisheries notes that CWC dominated communities should be considered as potential vulnerable marine ecosystems (VMEs), but without restricting this to any specified species or areas (UNGA 2007). The VME concept emerged from discussions at the United Nations General Assembly (UNGA) and gained momentum after UNGA Resolution 61/105. VMEs constitute areas that may be vulnerable to impacts from fishing activities. The UN Food and Agriculture Organisation (FAO) then listed criteria for how to evaluate areas including uniqueness, rarity, functional significance, or fragility. FAO guidelines state that identification of VMEs should be on a case-by-case basis, and regional fisheries management organisations worldwide have identified regionally relevant indicator species that support the recognition of cold-water coral VMEs (FAO 2019). However, these lists are often non-specific with generalised groups noted as potential VME indicator taxa. Furthermore, based on the FAO criteria, the International Council for the Exploration of the Sea (ICES) and regional fisheries commissions worldwide including the Northeast Atlantic Fisheries Commission (NEAFC) and the Northwest Atlantic Fisheries Organization (NAFO) have listed detailed VMEs and VME indicator species that are used for conservation in the high seas within the fisheries regions (Abril et al 2023; NAFO 2024). In the North Atlantic, the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) works to ensure the protection of deep-sea coral reefs; this is highly important for promoting conservation at the regional and national level, but does not list specific threats against corals (e.g. OSPAR 2009).

The IUCN Red List of Threatened Species (the "Red List") is one of the most highly recognised conservation tools in the world and represents a strong and effective communication tool to indicate the risks faced by global species (Rodrigues et al. 2006). It is also a species-level conservation tool, which assesses the potential extinction risk of individual species at the global level. Protecting deep-sea corals through their inclusion on the Red List will enhance global awareness, drive legislative action, and promote sustainable management practices crucial for preserving these irreplaceable ecosystems and their biodiversity.

Species-based conservation requires well-resolved taxonomy and taxonomic expertise. For deep-sea corals, this is often challenging because many species remain undescribed, as evidenced by new discoveries in the recent years (e.g. Saucier et al. 2017; García-Cárdenas et al 2019; Williams 2021; Kushida et al. 2024; Roberts et al. 2006; O'Hara et al. 2008). Modern surveys increasingly rely on underwater video imaging, often through remotely operated vehicles (ROVs), which has the advantage of being non-destructive and non-invasive, but species-level identification may be challenging or impossible from image data alone (e.g.

Horton et al. 2021). Image-based species-level identification of most CWCs is impossible because it relies on physical examination of the specimen, expert-based training, local knowledge (Henry and Roberts 2014), and often genetics (e.g. Radice et al. 2016). For octocorals, deep-sea images typically cannot resolve one of the main diagnostic characters for this group, the sclerites, which are calcium carbonate skeletal elements embedded into the soft tissue (Bayer et al. 1983). Much of deep-sea conservation approaches these habitats at the assemblage level, but this ignores the importance of species-specific life-history characteristics which contribute to overall resilient and robust ecosystems, and how differential responses and sensitivities of different species to disturbance and stress that may be unique. The Red List allows us to consider the risk to each species and how that can have cascading impacts on whole ecosystems.

In this study, our aim was to apply the IUCN Red List Categories and Criteria (IUCN 2012) to cold-water coral species to complement ongoing conservation efforts for these vulnerable species. We compiled complete assessments of 22 species of CWC species found in the North Atlantic, to establish a baseline for the approach of applying the Red List criteria to this important and vast area, the deep sea. The details of the relevant threats, and the specific impact of past and ongoing threats to each species, are publicly available in the published assessments, which are cited herein. This study aims to demonstrate the types of data available for deep-sea species, their limitations, and the interaction of these constraints with the Red List criteria. Our results highlight the impacts of cumulative habitat destruction in deep-sea ecosystems that can impact even widespread species.

Methods

Taxon selection

This paper represents a group effort resulting from a CWC Red List workshop held 14–17 September 2023 at the marine station in Sandgerði (Iceland). We initially selected a broad set of deep-sea CWC species collected by recent expeditions in and near Icelandic waters, especially the BIOICE (Benthic Invertebrates of Icelandic waters 1992–2004) and IceAGE (Icelandic marine Animals: Genetics and Ecology, ongoing since 2011) projects; the regional scope of these projects served as a starting point for species selection. The focal species presented an opportunity to assess an ecologically cohesive fauna; moreover, physical specimen material was accessible to examine in the course of discussions around potential taxonomic confusion. Our main specimen and information source was the invertebrate collection of the Icelandic Institute of Natural History (IINH, Gudmundsson 2024) along with the BIOICE database as well as the unidentified specimens of the IceAGE working collection housed at the DZMB (German Center for Marine Biodiversity Research; Senckenberg location Hamburg) and additional databases compiled by NOAA (National Oceanic and Atmospheric Administration; USA) and DFO (Department of Fisheries and Oceans; Canada). The direct access to specimens along with the expertise of participants led to a unique quality check of the taxonomic identifications for the Red List global assessment. We also favoured species that are listed at the species level as components of recognised VMEs. The final selection of 22 species was based on consensus expert opinion to identify candidate species with well-resolved species identification and range data, and treatment within recent taxonomic revisions and phylogenetic studies, from among species that occur in the NE Atlantic. These species do not represent a taxonomically or regionally comprehensive group, but rather a starting point to test the IUCN Red List criteria on cold-water corals as a group for which this approach has never previously been applied.

The Red List process is based on compiling the best evidence known for the species at the time. Species that are suspected by experts to represent multiple cryptic species could in theory be assessed by applying the Red List criteria. Such a species would be initially assessed over its total geographic, genetic, and/or morphological range, as a single species, with the expectation that later taxonomic revision could recognise additional lineages that required a new assessment or reassessment.

Though taxonomy is an ongoing science (Pante et al. 2015), a primary concern for the present study is that "lumping" multiple lineages together can give a false impression of resilience. The cryptic endemic local population is more vulnerable than it seems when it is misunderstood as being part of a larger, widespread and common species. In the case of CWCs, many of the distribution records are also based on identifications from video data or from bycatch. Since the present and past geographic ranges are highly relevant to assessing extinction risk, we consciously chose to focus on species where there was high confidence about the species identification in current and past distribution records.

Red List assessment

We assessed the extinction risk of each species using the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2012). This incorporated geographic distribution, population trend, and generation length.

Geographic range data were collected for each species from a combination of publicly available databases (e.g. GBIF, OBIS) and additional institutional or research databases including historical and recent literature and reports in local languages. Maps were checked by species experts responsible for the respective assessment, to flag possible misidentifications, erroneous coordinates, or doubtful records. All map data are now included with detailed metadata attached to each Red List assessment documentation with the IUCN. Point coordinate data were modified to polygon GIS information with a 1° buffer using QGIS (v.3.22.3-Białowieża; https://www.qgis.org/), and this polygon was used to calculate Area of Occupancy (AOO) and Extent of Occurrence (EOO) using GeoCAT (https://geocat.iucnredlist.org/).

Sessile colonial organisms cannot be usefully counted in terms of number of individuals, but population size is directly connected to the occupied range, AOO and EOO. Within the Red List criteria, the assessment of potential decline depends on an understanding of population size and potential changes within a timespan equivalent to three generations for the relevant species. Generation length was calculated based on the average age in a healthy population, or where possible based on fecundity and longevity data for the species, or from data for a closely related species as a proxy. Generation length in the scope of the IUCN Red List is preferably based on age of first reproduction added to a fraction of the length of the reproductive life for the species using the formula (Age of first reproduction + [0.5 × (length of the reproductive period)] (IUCN 2012). For colonial corals, the constant 0.5 is used, which is typically used for broadcast spawning species; age in the context of this equation refers to the age of the whole colony (Carpenter et al. 2008).

Where species cannot be assigned to a risk category, for example, where there is conflicting evidence about the impact of potential threats and/or high taxonomic uncertainty, the species is assessed as data deficient. These assessments evaluate the risk of total extinction for the species over its full global range.

Prior to publication on the global Red List (iucnredlist.org), each assessment was peer-reviewed by a taxonomic expert and by a Red List expert, to ensure that all relevant information was considered and that the criteria were correctly applied. In total, over 30 experts were involved as assessors, contributors, and reviewers in determining the Red List categories for the set of 22 species.

Results

Red List assessment overview

We completed the assessments of 22 species representing 15 taxonomic families, covering both stony corals (order Scleractinia) and octocorals (class Octocorallia), and a broad geographic scope. All species are present in the North Atlantic, but several species have much broader geographic ranges. Of the 22 selected species, 3 species (14%) were assessed as data deficient, 10 species (45%) were assessed as least concern, and 9 species (41%) were assessed in threatened or near threatened categories (Table 1). The single species in a threatened category is assessed as globally vulnerable: *Desmophyllum pertusum* (Linnaeus, 1758). All assessments in threatened or near threatened categories were made using Red List criterion A, based on evidence of past population declines.

Generation lengths calculated for the species in threatened and near threatened categories ranged from 7 to 20 years for most species, but up to 44 years for the octocoral *Primnoa resedaeformis,* Gunnerus, 1763, which has data indicating a relatively long age of more than 7 years before sexual maturity (Table 1). This means that for most species, the relevant time period to consider declines leading to assessment in a threatened category is from 21 to 60 years in the past.

Identified threats to these species that have caused damage in the past are mainly from bottom-contact activities, especially trawl fishing. In many cases, anecdotal or directly observed evidence from fisheries bycatch with accidental catch of corals serves as a proxy for estimating population density. Pollution is also a major threat: field studies in Norway have documented a reduction in growth and physical degradation of several CWC species found in proximity to salmon aquaculture cages (Wilding 2011; Kutti et al. 2015). Sediment plumes formed during hydrocarbon exploration or oil spills can also lead to octocorals overgrown with hydroids or covered by sediments (Etnoyer et al. 2016; Frometa et al. 2017).

The extent of population declines must be estimated based on evidence available for each species and the limitations of the available knowledge; thus, the process for determining the Red List outcome was tailored for each species. To illustrate the diversity of different assessment outcomes, we selected five species as case studies representing threatened, near threatened, least concern, and data deficient categories (Fig. 1). The examples are abridged and modified from the published Red List assessments that illustrate the specific approach used for each species.

Case studies

Desmophyllum pertusum (Linnaeus, 1758) (VU A2b)

Desmophyllum pertusum (previously classified as *Lophelia pertusa,* Addamo et al. 2016 is a hard coral and is the dominant species in Atlantic deep-sea coral reefs often called "*Lophelia*" reefs. The species is widely distributed throughout the North Atlantic, typically at depths from 40 to 1300 m (Davies et al. 2008), in waters with temperatures of 4–12 °C (Roberts et al. 2006). This assessment was explicitly limited

Table 1 The 22 cold-water coral species assessed for the IUCN global Red List. The full assessments have been published at www.iucnredlist.org. Generation length was calculated as Age of first reproduction + [$z \times$ (length of the reproductive period)], for all species here the parameter $z = 0.5$ is used as this is considered appropriate for broadcast spawning species, and the length of the reproductive period is maximum age minus age of first reproduction where additional demographic information is not available (IUCN 2012)

Class	Classification	Species	Global IUCN Red List status	Reference	Generation length estimate	National / Regional Red List outcomes
Hexacorallia: Scleractinia	Caryophylliidae	*Desmophyllum dianthus* (Esper, 1794)	LC	Wessels et al. (2024)		Norway: DD, Mediterranean: EN
		Desmophyllum pertusum (Linnaeus, 1758)	**VU A2b**	Morrissey and Allcock (2024)	The age at first maturity of reef-building corals is three to 8 years in warm water (Wallace 1999). Cold-water corals are expected to live longer. The average length of one generation is at minimum 10 years (IUCN 2012): **10 years**	Norway: NT, Mediterranean: EN
	Dendrophylliidae	*Enallopsammia profunda* (Pourtalès, 1867)	**NT A2b**	Morrissey (2024)		-
		Enallopsammia rostrata (Pourtalès, 1878)	LC	Korfhage and Morrissey (2024)		-
Octocorallia: Malacalcyonacea	Alcyoniidae	*Anthothela grandiflora* (Sars, 1856)	LC	Allcock (2024)		Norway: NT
	Victorgorgiidae	*Trachythela rudis* Verrill, 1922	LC	Allcock and Morrissey (2024)		-
Octocorallia: Scleralcyonacea	Anthoptilidae	*Anthoptilum murrayi* Kölliker, 1880	DD	Neves and Ólafsdóttir (2024)	Average age of 6.5 years, from a population with age estimates 6–17 years (García-Cárdenas and López-González 2022). Minimum age at maturity is ~6 years, estimated lifespan estimated at least 20 years. Generation length = 6 + [0.5 × (20 − 6)] = **13 years**	-
	Balticinidae	*Balticina christii* (Koren & Danielssen, 1848)	DD	Sigwart and Allcock (2024)		Norway: LC
	Chrysogorgiidae	*Radicipes gracilis* (Verrill, 1884)	LC	Barnhill et al. (2024)		Norway: VU
	Coralliidae	*Heteropolypus sol* Molodtsova, 2013	LC	Morrissey et al. (2024)		-

Table 1 (continued)

Class	Classification	Species	Global IUCN Red List status	Reference	Generation length estimate	National / Regional Red List outcomes
		Paragorgia arborea (Linnaeus, 1758)	**NT A2b**	Sigwart et al. (2024)	Red List assessment for Norway calculated the generation time for *P. arborea* as 20 years (Tandberg and Mortensen 2021): **20 years**	Norway: NT
		Paragorgia johnsoni Gray, 1862	**NT A2b**	Sampaio et al. (2024)		Norway: LC
	Funiculinidae	*Funiculina quadrangularis* (Pallas, 1766)	**NT A2bc + 4c**	Everett and Nascimento (2024a)	Maturity at 6 or 7 years, assumed longevity of ~ 30 years (Greathead et al. 2007, Greeley 2022). Generation length = 7 + [0.5 × (30 − 7)] (rounded up) = **19 years**	Norway: LC, Mediterranena: VU
	Gyrophyllidae	*Gyrophyllum hirondellei* Studer, 1891	LC	Sampaio and Arantes (2024)		-
	Kophobelemnidae	*Kophobelemnon stelliferum* (Müller, 1776)	**NT A2bc**	de Montety and Barnhill (2024)	Based on ecologically similar species (e.g. *Funiculina quadrangularis*, *Pennatula aculeata*) as a proxy: **19 years**	Norway: LC, Mediterranean: LC
	Pennatulidae	*Pennatula aculeata* Danielssen, 1860	**NT A2ab + A4c**	Allcock and Sigwart (2024)	Maturity at 7 or 8 years, and assumed longevity of ~ 30 years (Greathead et al. 2007, Greeley 2022). Generation length = 8 + [0.5 × (30 − 8)] **= 19 years**	Norway: LC, Mediterranean: DD
		Pennatula phosphorea Linnaeus, 1758	**NT A2bc + A4c**	Neves and Sigwart (2024)	Based on the congener *P. aculeata* as a proxy: **19 years**	Mediterranean: VU
	Primnoidae	*Candidella imbricata* (Johnson, 1862)	LC	Klubb and Morrissey (2024)	-	-
		Convexella jungerseni (Madsen, 1944)	DD	Morrissey and Barnhill (2024)	-	-

Table 1 (continued)

Class	Classification	Species	Global IUCN Red List status	Reference	Generation length estimate	National / Regional Red List outcomes
		Primnoa resedaeformis (Gunnerus, 1763)	**NT A2bc + A4c**	Everett and Nascimento (2024b)	Age at first reproduction 7.6–19.8 years in this species and lifespan up to 80 years in the sister species *P. pacifica* (Mercier and Hamel 2011, Fountain et al. 2019, Choy et al. 2020). Minimum generation length = 7.8 + [0.5 × (80 − 7.8)] (rounded up) = **44 years**	Norway: LC
	Protoptilidae	*Distichoptilum gracile* Verrill, 1882	LC	Morrissey and Bax (2024)	-	-
Octocorallia	Ceratocaulidae	*Ceratocaulon wandeli* Jungersen, 1892	LC	Ólafsdóttir and Sigwart (2024)	-	-

in scope to the population of *D. pertusum* in the Atlantic, as records from other regions may not represent the same lineage. Nonetheless, its range extends from the southwestern Barents Sea to West Africa on the eastern Atlantic margin and from Nova Scotia down the western Atlantic margin into the Gulf of Mexico. It also occurs off oceanic islands, such as the Azores, Canary Islands, and Madeira, and along the southeastern slope of Brazil (Davies et al. 2008).

This species can form long-lived framework structures that provide habitat for other organisms, increasing local biodiversity (Jensen and Frederiksen 1992; Jonsson et al. 2004; Costello et al. 2005; Roberts et al. 2006; Lessard-Pilon et al. 2010; Benfield et al. 2019). Growth rates vary, but are generally slow, and large-scale reefs may form over thousands of years (Roberts 2009). *Desmophyllum pertusum* has been significantly impacted by trawling (Rogers 1999; Hall–Spencer et al. 2002; Buhl-Mortensen et al. 2017; Buhl-Mortensen 2017), with studies indicating that up to 50% of reef areas on the Norwegian margin have been damaged by trawl gear (Fosså et al. 2002). Similar impacts are suspected throughout its range since the expansion of deep-water fisheries in the late twentieth century. In some regions, recent surveys have identified clear evidence of mechanical damage in the recent past from breakage patterns in remaining coral rubble (Grehan et al. 2004). Evidence from trawl fisheries provides an index of damage that is relevant to this species. Moreover, oil and gas drilling is a threat of major concern to this species in Africa, Brazil, and the USA and that is expanding in the South Atlantic (off the coasts of Brazil, Namibia, and South Africa) and in the Caribbean. In total, given that damage is likely at these levels or higher on average across the full range of the species, this indicates the destruction or severe degradation of at least 30% of the reefs in the last 30 years. For a sessile species that is the dominant member of reefs, the loss of these reefs is a direct measure of population decline. The threats also are projected to continue, as substantial areas of known *D. pertusum* reefs are not in protected areas (OSPAR 2022; Howell et al. 2022). Climate change is also a threat, and worst-case parameters in modelling studies predict up to 85% of reefs at risk by 2060 (Ross and Howell 2013; Jackson et al. 2014; Morato et al. 2020). A population loss of 30% within three generations is the threshold for the vulnerable category; here, the 10-year generation length is certainly a conservative under-estimate. *Desmophyllum pertusum* was assessed as vulnerable (Morrissey and Allcock 2024).

Paragorgia arborea (Linnaeus, 1758) (NT A2b)

Paragorgia arborea is a very large, bright pink or white gorgonian coral that lives in cold waters in the North and South Atlantic and South Pacific (Sánchez 2005; Herrera et al. 2010). It serves as a foundation species in coral garden

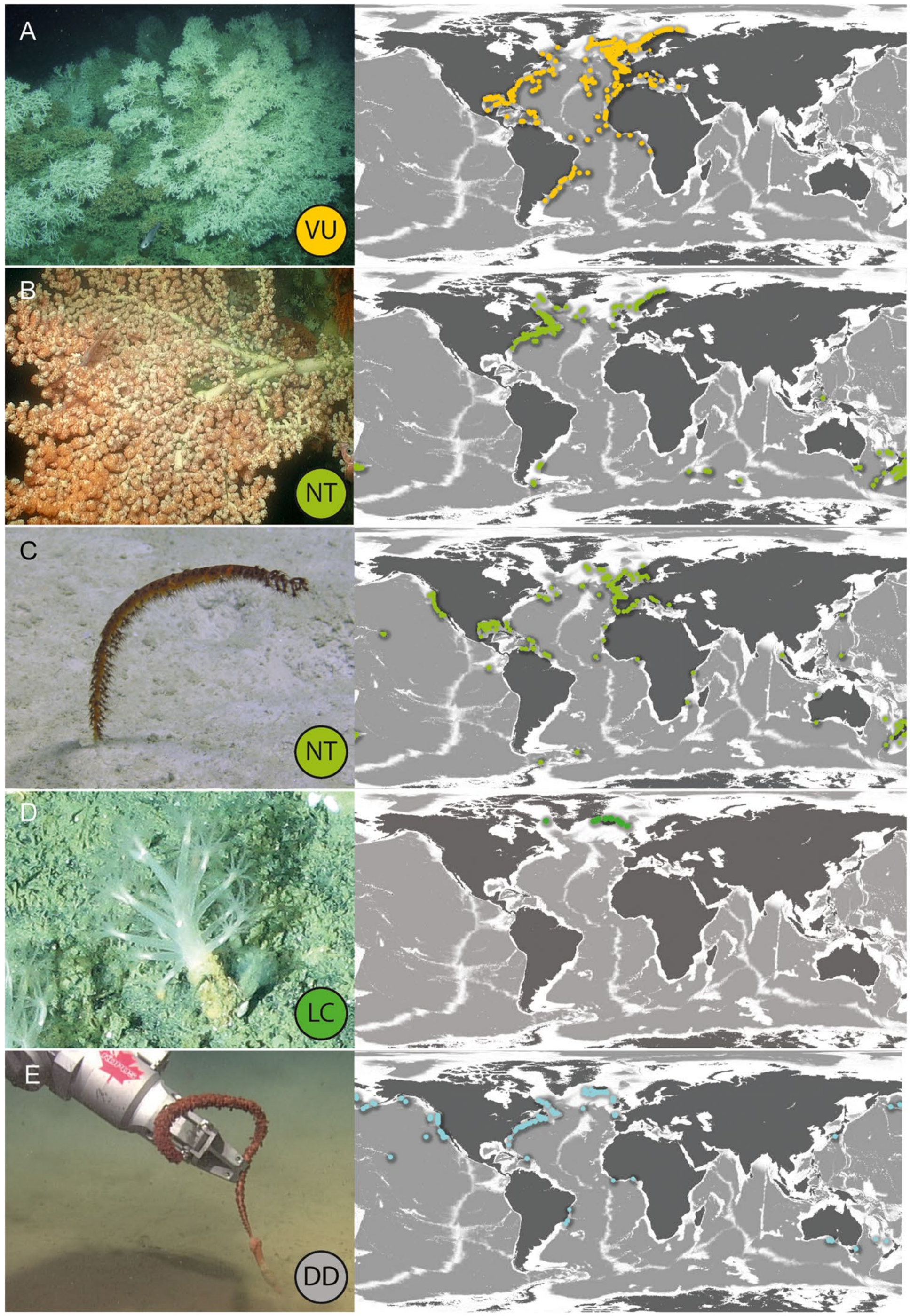

Fig. 1 Photographs (left) and distribution maps (right) for the five species highlighted as case studies in the present work. **A** *Desmophyllum pertusum*, photo: Marine Institute, Ireland; **B** *Paragorgia arborea*, photo: Fisheries and Oceans Canada (DFO-NL), Nunatsiavut Government, and Amundsen Science; **C** *Funiculina quadrangularis*, photo: Marine Institute, Ireland; **D** *Ceratocaulon wandeli*, photo: Marine and Freshwater Research Institute (MFRI Iceland) (López-González et al. 2024); **E** *Anthoptilum murrayi (species ID was confirmed from the collected specimen)*, photo: CHONe-DFO-CSSF, Canada. Maps prepared by Mark E. de Wilt

habitats, providing habitat complexity with its large size and three-dimensional structure. It typically resides at depths of 1000–2000 m, but can be found as shallow as 40 m in fjords and as deep as 3000 m (Buhl-Mortensen et al. 2015). *Paragorgia arborea* has been suggested to be a brooding species based on recruitment patterns (Lacharité and Metaxas 2013), but this has yet to be confirmed. It is sensitive to sediment type, which is impacted by bottom-contacting activities, meaning it has very low and potentially declining recruitment potential. Colonies have growth rates of about 1–1.6 cm per year (Mortensen and Buhl-Mortensen 2005; Sherwood and Edinger 2009), which slows down after 20 years (Mortensen and Buhl-Mortensen 2005). Colonies of *P. arborea* can be more than 3 m tall (Tendal 1992), suggesting they may be centuries old. A regional Red List assessment for Norway calculated the generation time for *P. arborea* as 20 years (Tandberg and Mortensen 2021), but this is likely an under-estimate. The Norwegian national

Red List assessment states that they used data on the age of polyps within a colony (Tandberg and Mortensen 2021), whereas the standard IUCN method for corals considered the whole colony as the mature individual for calculating generation length (Carpenter et al. 2008). The global assessment used the Norwegian generation length for consistency; however, this is a conservative under-estimate. The minimum relevant period for the Red List assessment (3 generations) is 60 years or a timespan starting in the 1960 s.

Regional Red List assessments indicate significant declines in some areas (Table 1). The extent of damage is also inferred from trawling bycatch; declining frequency in bycatch and the declining size of individuals is evidence of population decline. The cumulative impact of those declines suggests a global decrease in the world population of at least 20%. *Paragorgia arborea* is a slow-growing species that can live for centuries, and its fragile skeleton breaks easily upon physical/mechanical contact and cannot readily recover (Mortensen and Buhl-Mortensen 2005; Sundahl et al. 2020). Since parts of the population are not protected from ongoing threats, and the evidence for past decline is based on bycatch data that indicates a large decline but under 30%, the species was assessed as near threatened (Sigwart et al. 2024).

Funiculina quadrangularis **(Pallas, 1766) (NT A2bc)**

This sea pen is distributed worldwide, except in the Arctic, and occurs at depths from 20 to 3600 m, with the majority found shallower than 500 m. It has a scattered distribution but forms clusters in soft sediment habitats and is locally relatively common where it still occurs (Ager and Wilding 2009; Gili and Pages 1987; Ocaña et al. 2000). Sea pen species are generally slow growing and can live for several decades (Wilson et al. 2002; Neves et al. 2015). The generation length was calculated based on an age of maturity at 6 or 7 years and an assumed longevity of ~30 years (Greathead et al. 2007; Greeley 2022; Table 1). The Red List assessment is based on changes in the past three generations, the ~55 years since the 1960 s.

Reduction in population has been documented at regional scales worldwide, often associated with trawl fishing pressure (Anderson et al. 2023; Martinelli et al. 2023). The species is commonly caught as bycatch in demersal trawl fisheries globally (NOAA DSCRTP 2016; Anderson et al. 2023), indicating ongoing damage to the populations at a large scale. Damage from trawling eliminates mainly large and reproductively mature colonies (Macdonald et al. 1996). Regional declines are estimated at around 40% in the Mediterranean and near total removal in the North Sea (Fabri et al. 2014; Downie et al. 2021). Substantial reductions are inferred in the Gulf of Mexico (Zimmerman et al. 2020) and other areas, reflecting global declines due to fishing impacts on coastal shelves.

This species is not known to retract into the seabed (as some other sea pens do), meaning it does not actively avoid trawl nets, and impacts can break their long and delicate axial rod. Genetic studies show high gene flow consistent with a highly fecund, broadcast spawning species (Wright et al. 2015). Its global distribution provides a large reservoir population that could facilitate recolonization of impacted areas if fishing pressure is removed (Greathead et al. 2007; Pierdomenico et al. 2018; Martinelli et al. 2023).

The global decline is suspected to be at least 25%, with higher regional declines. Because the global population decline is approaching but does not exceed the 30% threshold for vulnerable, *Funiculina quadrangularis* was assessed as near threatened (Everett and Nascimento 2024a).

Ceratocaulon wandeli **Jungersen, 1892 (LC)**

This cold-water soft coral is an Arctic endemic species, found in large fields in deep waters north of Iceland with patchy records elsewhere. It is mainly found at depths of 525–850 m (Williams 1987) but extends to 2000 m. It represents a phylogenetically distinct species and was recently re-classified in the new monotypic family Ceratocaulidae (López-González et al. 2024). Its distribution appears to follow the Iceland-Faroe Slope Jet current. This oceanographic current was described only recently and runs from northern Iceland east to the Faroe Islands (Semper et al. 2020). Nevertheless, the species has recently been reported in Davis Strait (eastern Canadian Arctic) indicating that the East and West Greenland currents also play a role in its dispersal (Neves et al., unpublished). The coral thrives in very cold, deep waters, with temperatures mostly below 0 °C, and cannot tolerate temperatures above ~2.5 °C.

Ceratocaulon wandeli is relatively small, the whole colony is less than 10 cm when fully extended, and it attaches to boulders, cobbles, or smaller rocks, with the colony partly embedded in sparse mud. The species has a distinctive morphology with a thick cuticular sheath surrounding the stalk of the colony, and large retractable polyps (López-González et al. 2024). Despite an area of occupancy smaller than 2000 km^2, there is no evidence of decline or significant population fragmentation. The depths of the current population in Iceland are deeper than any current fishing activity. There is no current evidence of bycatch in commercial trawling in Icelandic waters where it is abundant. *Ceratocaulon wandeli* was assessed as least concern (Ólafsdóttir and Sigwart 2024).

Anthoptilum murrayi Kölliker, 1880 (DD)

This sea pen has a global distribution, inhabiting depths of 155–2500 m and primarily lives on soft bottom habitats. It has been reported from mainly continental slope areas off the northeast coast of North America, the North Atlantic, the South Atlantic, New Zealand, West Africa, the Caribbean, and the Indo-Pacific. *Anthoptilum murrayi* has a patchy distribution and can form large populations. The species reproduces by broadcast spawning, and the eggs are relatively large (Pires et al. 2009). It is generally highly fecund, but with strong regional differences; for example, fecundity was almost double in Brazil (Pires et al. 2009) compared to Iceland (García-Cárdenas and López-González 2022). In Iceland, age estimates for mature colonies were 6–17 years old, and growth rates were slow (0.10–0.17 mm per year) (García-Cárdenas and López-González 2022). The species likely lives typically longer than 20 years.

Anthoptilum murrayi is impacted by bottom trawling, which occurs throughout its global range except in a few protected areas. Like *F. quadrangularis*, this species is not known to withdraw into the sediment. Recovery from such damage is slow, potentially taking decades, given the species' slow growth and long lifespan. Given the extremely broad distribution of the species and the lack of data on specific threat impacts in more than half of its range, it is currently impossible to quantify or estimate the scale of potential global-level declines within the timespan relevant for the Red List assessment, which is a period of only the last ~21 years (Table 1). *Anthoptilum murrayi* was assessed as data deficient due to a lack of data on historical population size and trends but high level of concern for likely threat impact that is currently unquantified (Neves and Ólafsdóttir 2024).

Discussion

Cold-water coral species are increasingly recognised as ecosystem engineers of important and vulnerable marine habitats (Roberts 2009). They have been recognised as vulnerable to direct damage from fisheries for many years at an international level. In this study, we selected a set of species for which there is some published information regarding their biology (e.g. growth rates, longevity, reproduction), with a well-resolved taxonomy (i.e. major taxonomic issues unknown), and widespread distribution. There are several thousand CWC species currently described (Roberts 2009). Many of the coral species found in the Northeast Atlantic deep sea have very broad distributions, extending across the Atlantic basin, or to the southern hemisphere or even to the Pacific. Thus, it would be expected that many species are not assessed in threatened categories under the IUCN Criteria, because a broad range naturally buffers the risk for a species in terms of its potential global extinction. The fact that > 30% of the species we assessed are facing an elevated estimated risk for global extinction is a sobering reflection of the extreme destruction of deep-sea habitats, which so often goes unnoticed.

Although climate change is a major threat to these species, it is included only indirectly in global Red List assessments. While climate warming impacts in the deep sea are more difficult to model than in shallow waters (Pampoulie et al. 2024), it is clear that temperature is also rising in the deep ocean (Brito-Morales et al. 2020). Cold-water coral species are clearly sensitive to temperature, and ocean warming will alter the distribution of suitable habitat for these sedentary organisms. Species and populations may have differing sensitivity to changes in seawater chemistry; most corals have calcium carbonate skeletons (or skeletal parts) composed of aragonite or calcite. The skeletons of scleractinians are typically composed of aragonite while those of hydrocorals and octocorals (including sea pens) are typically calcitic (e.g. Williams 2011; Neves et al. 2018). The potential impacts from mineral dissolution as climate change lowers the ocean pH may be more severe for corals with aragonitic skeletons, as aragonite is more soluble than calcite (Mucci 1983). These impacts are region specific, which also complicate predictive modelling. For instance, in the North Atlantic, the calcite saturation horizon is very deep below seafloor depth in the eastern North Atlantic, rising to c. 4500 m in the west) compared with 2500 m for the aragonite saturation horizon off the coast of Iberia (Sulpis et al. 2018, Fontela et al. 2020). In addition, calcite and aragonite saturation depths can be significantly shallower in other regions of the North Atlantic (e.g. Davis Strait and Baffin Bay, NW Atlantic, Azetsu-Scott et al. 2010).

The IUCN global Red List provides a metric for the risk of total extinction for the species (Rodrigues et al. 2006; Carpenter et al. 2008; Gutierrez et al. 2024). For widespread species, this can seem to mask potential damage at local and regional scales. Several of the species that we assessed as part of this project had also been previously assessed within the regional Red List for the Mediterranean using the IUCN criteria. For example, *Desmophyllum pertusum*, assessed as globally vulnerable, was assessed as endangered in the Mediterranean (Orejas et al. 2015).

Because of the ecological importance of *D. pertusum* reefs, there has been extensive research on the extent and condition of these habitats and legislation to protect them. The known range of *D. pertusum* has expanded in recent years due to targeted research. Models predicting potential habitat space for *D. pertusum* showed that around 40% of potential populations in the UK and Ireland likely occurred inside marine protected areas, although this was an average between very high coverage of UK populations and low coverage of Irish populations (Howell et al. 2022). At a larger scale, over 70% of *D. pertusum* reefs in the OSPAR Maritime Area in the NE Atlantic are outside protected areas (OSPAR 2022). The only known *D. pertusum* reef in eastern Canada (NW Atlantic) is part of the Eastern Canyons Conservation Area, an OECM (Other effective area-based conservation measure) where bottom trawling activities are prohibited (e.g. Beazley et al. 2021; DFO 2025).

In some areas, *D. pertusum* reefs are relatively well mapped because they are formed of large-scale framework structures that build up vertically over generations. These skeletons directly interfere with bottom-contact fishing activities, and this impact leaves evidence in the form of damaged reefs and coral rubble (Fosså et al. 2002). The widespread fields of coral rubble in the North Atlantic provide evidence of the scale of this species' global decline in the last three glacial-interglacial cycles (Frank et al. 2011).

The large octocoral *Paragorgia arborea* is an indicator species for cold-water coral VMEs in different national and international listings including in the OSPAR designation "Coral gardens" (OSPAR 2022) and "large gorgonians" in NAFO (NAFO 2024). *Paragorgia arborea* is mainly known from areas with steep rock faces and fast flowing currents, such as undersea canyons and fjords, making it challenging to sample and monitor (Watanabe et al. 2009; Sundahl et al. 2020).

Both *D. pertusum* and *P. arborea* are likely to be highly sensitive to temperature and as sessile colonies that live for over 100 years, they cannot easily retreat from rising sea temperatures. Climate pressures could lead to 99% reduction in available habitats for *P. arborea* (Morato et al. 2020) and 85% reduction of NE Atlantic *D. pertusum* reefs (Ross and Howell 2013; Jackson et al. 2014) in worst-case scenarios. The two species can be large ecosystem engineers that can structure local habitats, and their size and distinctive natures make them relatively easy to confidently identify to the species level.

The sea pen species we assessed showed some of the most surprising levels of past decline, mainly based on the local extinction and range reduction, or from proxy evidence such as a history of frequent bycatch in areas where the species are now relatively rare or sparsely distributed. The two case studies highlighted here illustrate the potential confounding factors to assessing sea pen declines. *Funiculina quadrangularis* and *Anthoptilum murrayi* are ecologically similar, but the former species has extensive documentation with records of it appearing in bycatch. *Funiculina quadrangularis* is relatively easy to identify globally, because of its distinct quadrangular axial rod. *Anthoptilum murrayi* by contrast is more easily confused with other *Anthoptilum* species, consequently there is less clarity about historical population trends. Sea pen habitats are also noted as VMEs that are threatened by fishing activity (Grinyó et al. 2020; Downie et al. 2021; Martinelli et al. 2023), and that must be better understood and protected considering their role as habitat for other species, including fish larvae and juveniles, as well as invertebrates (e.g. Baillon et al. 2012; Boulard et al. 2023, 2024).

Some conservation measures are already in place for deep-sea habitats, with new candidate marine protected areas and other conservation zones proposed in deep waters of several countries. The European Union has closed some areas to deep-sea fishing and has implemented a trawling ban below 800 m since 2017 (EU 2022), but such protection is not universal and does not protect many species that occur in shallower waters or in international waters. These assemblages are recognised at habitat level, but many of the constituent species are poorly studied.

The IUCN global Red List is a species-based conservation tool, so it necessarily requires good knowledge of the species as a basis, which can come from scientific experts with diverse backgrounds (Tomasini 2018). Access to expertise presents a significant challenge for assessment of many marine invertebrate species, where species-level identification often depends on examination of microscopic characters. Marine species are among the groups that are significantly under-represented on the Red List (Bachman et al. 2019; Sigwart et al. 2023). Modern surveys rely heavily on underwater imaging, which has revolutionised the scientific and public understanding of these ecosystems; however, image data are usually insufficient for species identification. Expert vetting of the available distribution records was a key part of our process to compile the maps that underpin the Red List assessments for this first set of coral species inhabiting the deep sea. Most conservation actions for CWCs to date have focused on ecosystem or habitat protection and recognition as VMEs. The Red List offers an important complementarity to recognise how threats impact individual species in different ways. This work provides a starting point, but further work on CWC assessment is clearly urgently needed, as is a better understanding of their biology and ecology. Species with wide distribution ranges that are globally threatened provide a strong indication of the need for further conservation to protect these sensitive species throughout their ranges.

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