



## REVIEW ARTICLE

# Critical knowledge gaps in the conservation and restoration of cold-water corals

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### Abstract

**Introduction:** Critical knowledge gaps hamper effective conservation of threatened cold-water coral (CWC) ecosystems, facing cumulative anthropogenic and climate pressures. This review provides a strategic roadmap for urgent, informed intervention.

**Objectives:** This review synthesizes global expert consensus to identify and prioritize key knowledge gaps impeding CWC conservation and restoration. Our objective is to provide a strategic roadmap for research, funding, and policy over the next decade.

**Methods:** Through literature synthesis and a global expert panel (i.e. the authors), we identified and prioritized critical knowledge gaps in CWC conservation and restoration. Priorities were defined as challenges addressable within a decade through focused international collaboration and funding.

**Results:** We identified 10 knowledge gaps across five themes, including CWC status and distribution, community composition, early life history, metapopulation dynamics and connectivity, growth, and food dynamics. We then provide recommendations for international policy that would support CWC protection.

**Conclusions:** Addressing these research priorities is a prerequisite for effective conservation strategies. A coordinated international effort is crucial over the next decade to translate this knowledge into actionable plans and prevent irreversible biodiversity loss.

**Implications for Practice:** Conservation and restoration of slow-growing cold-water coral (CWC) is hampered by a lack of basic biological data, particularly regarding distribution, early life history, population connectivity, growth, and trophic ecology. Future efforts must prioritize this research to develop viable techniques and protect critical larval source populations. CWC recovery spans decades to centuries, a timescale fundamentally misaligned with typical project durations, which are often constrained by short-term funding cycles (e.g. 3–5 years). Therefore, establishing internationally coordinated, long-term monitoring programs at both restoration and natural reference sites is essential to accurately measure success. While universal monitoring duration is scientifically premature, programs must be planned on a multi-decadal scale (e.g. 20–50 years) to capture key ecological milestones.

**Key words:** cold-water coral, conservation and restoration, early life history, habitat distribution, population connectivity, trophic ecology

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Kristopher Benson declares that the scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the U.S. Department of Commerce.

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## Introduction

Cold-water corals (CWC: see Box 1) provide significant ecosystem functions in the deep-sea (Rogers 1999; Buhl-Mortensen et al. 2010) but despite their ecological importance, CWC face threats from various human activities, such as bottom fishing (Clark et al. 2016), oil pollution (e.g. *Deepwater Horizon* oil spill) (Girard & Fisher 2018), deep-sea mining (Carreiro-Silva et al. 2022), and climate change (Morato et al. 2020; Ross et al. 2020). Their vulnerability is aggravated by the fact that they are largely unknown or poorly mapped in most regions and often discovered after they have already sustained substantial damage (Hall-Spencer et al. 2022). Consequently, several CWC taxa (alongside vent systems and sponges, which have similar conservation challenges) have been identified as indicator species for classifying vulnerable marine ecosystems (VMEs; United Nations General Assembly Resolution 64/72), and the role of their conservation to protect marine benthic biodiversity is widely recognized. Preventing damage to an ecosystem is preferable to trying to restore it. This is particularly important for CWC, where restoration is logistically challenging (Da Ros et al. 2019) and recovery may take thousands of years (Roark et al. 2009; Prouty et al. 2017; Montseny et al. 2021). Consequently, emphasis has been placed on protecting them from the most damaging human activities within national waters, as well as in areas beyond national jurisdiction (Food and Agriculture Organization [FAO] 2016; Open Ocean Trustee Implementation Group [OOTIG] 2019) through establishing marine protected areas (MPAs) (Jackson et al. 2014; Huvenne et al. 2016; Sink et al. 2023) or other conservation measures (Beazley et al. 2021; Otero & Marin 2019). However, given the ongoing threats, it is also essential to develop active restoration methodologies to serve as necessary tools for repairing already damaged systems and mitigating further loss. There have been few attempts at active

restoration, or assisted regeneration, of damaged/degraded CWC habitats, with variable results, mostly on a small scale (e.g. Brooke et al. 2006; Boch et al. 2019; Montseny et al. 2021).

This review seeks to identify existing knowledge gaps and key scientific, technological, and economic challenges through assessing the present state of knowledge of CWC conservation and restoration. Additionally, we construct a roadmap to provide recommendations for prioritizing future research directions and specific areas for investment development. The overall view of this review is shown in Figure 1.

## Methods

A workshop on CWC ecosystems was held on the May 10th–12th 2023 at the Engineerium Centre (<https://www.engineerium.no/>) in Fomebu, Lysaker, Norway, hosted by REV Ocean. It was attended by 25 subject matter experts representing 13 countries in Europe, America, Africa, and Asia. Attendees included early-to senior-career individuals and included expertise in CWC ecology, conservation, restoration, reproduction, taxonomy, phylogenetics, microbiomes, and geochemistry, as well as policymakers and marine resource managers. The research priorities analyzed in this review were identified through the structured 2.5-day expert workshop. To establish a common baseline, a summary report on the current knowledge of CWC ecology, conservation, and restoration practices was circulated to participants beforehand. The workshop agenda was anchored by expert presentations, which framed the subsequent collaborative sessions. Participants worked in breakout groups to generate a list of knowledge gaps, which were then systematically collated and synthesized into four overarching themes. A voting exercise was then conducted, where each attendee used four votes to identify the most critical gaps or challenges. The 10 knowledge gaps and six challenges (Table 1 and

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### Box 1. A definition of “cold-water coral”

The wide range of ocean conditions on our planet and the diverse adaptations that enable corals to survive in these environments present a significant challenge in providing a concise description that encompasses the various types of cold-water corals. Consequently, the term “cold-water coral” (CWC) serves as a blanket term for a multitude of coral taxa that occupy different habitats beyond the warm, sunlit waters inhabited by tropical zooxanthellate corals (i.e. those that have symbiotic dinoflagellates). Conventionally, CWC include Octocorallia, some Hexacorallia, and at least one family of Hydrozoa, the Stylasteridae (lace corals). This terminology has been applied to “deep-water corals,” even though the same taxa can be found in shallow polar seas, which is a phenomenon called cold-water/deep-water emergence (Hessler 1970; Häussermann et al. 2021). It has also been used to refer to any corals found in cold “deep” water. The threshold for the “deep sea” is often considered to be 200 m, but in some regions, “deep water” may not necessarily equate to cold water. For instance, in the Red Sea, azooxanthellate corals can be found in 22°C water down to 100 m (Roder et al. 2013). It is, therefore, beneficial to have a unified definition that encapsulates this complexity. We propose the following definition:

Acknowledging that exceptions are common in biology, we propose that the term “cold-water coral” (CWC) describes all corals that do not harvest light (azooxanthellate) or are facultatively zooxanthellate (e.g. *Oculina varicosa*). This definition would typically include deep/CWC and exclude the majority of warm-water corals found shallower than 30 m depth (i.e. those having symbiotic dinoflagellates), while acknowledging the possibility of exceptions in biology.

We believe this operational description covers most species that researchers refer to as deep/CWC, and we hope, therefore, that it will be adopted by the scientific community. A single description is, after all, important in terms of public outreach and informing policy, making this ecosystem more accessible to non-specialists. It is important to note that this does/should not replace secondary descriptors (i.e. deep-sea; deep-water emerged; etc.) in the peer-reviewed literature where needed to describe specific habitats/species.

Supplement S1) that garnered the highest cumulative vote counts were subsequently selected as the focus of this review.

## Critical Scientific Knowledge Gaps in CWC Conservation and Restoration

### CWC Status and Distribution

**Prioritized Knowledge Gap 1: the Global and Regional Distribution Patterns of CWC.** CWC represents thousands of species

with varied habitats and distributions around the globe, ranging from continental shelves to abyssal depths (Fig. 2). However, CWC global and regional distribution patterns have not been studied comprehensively (Supplement S2). The distribution patterns of CWC depend largely on the species and types of assemblages or communities likely to be prevalent in different areas, such as CWC reefs, CWC garden habitats, and sea pen fields (Cordes et al. 2023). Information on the distribution of these communities, including information on their extent, diversity, and density of component species, is key to understanding their value and guiding

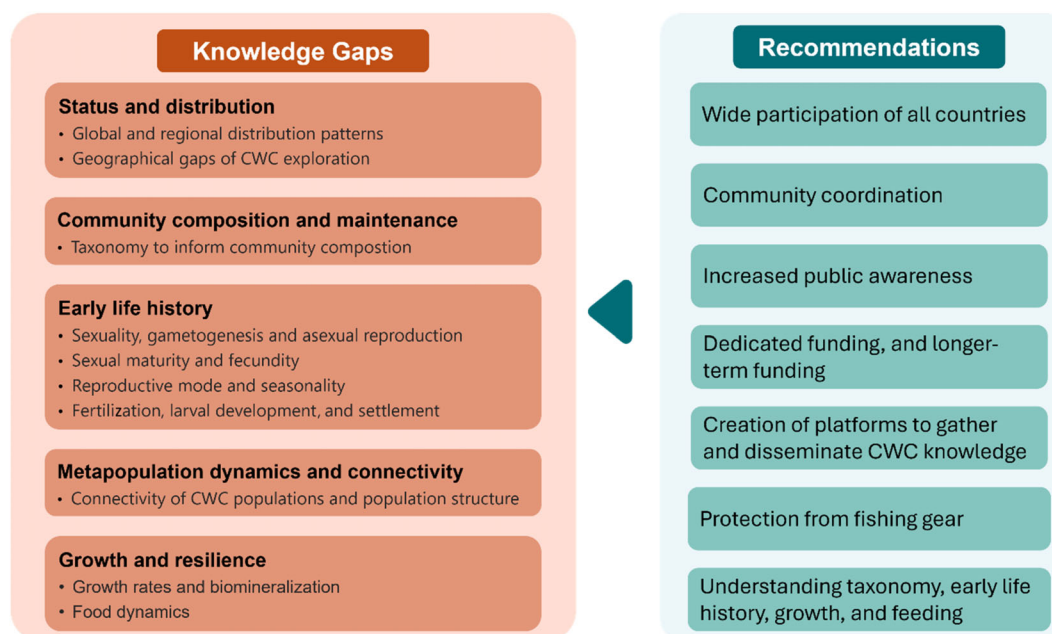


Figure 1. Knowledge gaps and corresponding recommendations for cold-water coral conservation and restoration.

**Table 1.** Overarching priorities and challenges for CWC conservation and restoration. Note: please refer to Supplement S1 for detailed discussions.

Overarching priority/ challenge	Identified limitations and barriers	Proposed solutions and strategic actions
(1) Capacity development and equity	<i>Financial and technical:</i> Research requires sophisticated, expensive vehicles, limiting access to high-income nations. <i>Geographic bias:</i> Clear “regional bias” in research, with limited capacity in Low- and Middle-Income Countries (LMICs) and for Indigenous Peoples.	<i>Knowledge exchange:</i> Support knowledge exchange, training, and research opportunities for LMICs. <i>Affordable tech:</i> Promote and expand affordable deep-sea technologies (e.g. low-cost camera systems). <i>Equitable access:</i> Ensure equitable access to the deep-sea as a “global common” via shared archives and expeditions.
(2) Bottom trawling	<i>Scale of damage:</i> Bottom trawling is the most widespread and damaging activity to CWC habitats. <i>Knowledge gaps:</i> Poor knowledge of CWC distribution limits impact estimation and protection.	<i>Prohibition:</i> Cease bottom-trawl fishing in areas of CWC occurrence. <i>Identify refugia:</i> Prioritize science to identify non-trawled locations to serve as natural reference areas and inform spatial protection.
(3) Community and funding coordination	<i>Lack of coordination:</i> A united approach to common global issues is lacking. <i>Funding instability:</i> Funding cycles are often too short or intermittent. <i>Logistical hurdles:</i> Different national legal frameworks (e.g. for genetic resources) hinder collaboration.	<i>Unified platform:</i> Create an online forum for researchers, policymakers, and managers to promote collaboration, data sharing, and knowledge exchange. <i>Funding strategy:</i> Improve engagement with funding agencies and use proactive planning to support research continuity.
(4) CWC sample/specimen rescue	<i>“Dark Materials”:</i> Vast quantities of specimens are stored locally (“dark materials”) and are not in accessible, cataloged collections. <i>Lack of funding:</i> Long-term preservation is often not financed in grants. <i>Expertise and legal gaps:</i> Reductions in taxonomists and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulations on sample sharing create bottlenecks.	<i>“Sample Rescue” activities:</i> Urgently deploy activities to catalog “dark coral materials” and metadata and accession them into curated, accessible collections. <i>Focus on taxonomy:</i> Increase financial and institutional support for taxonomy. <i>Improve policy:</i> Improve CITES science exemptions and international coordination of collections.
(5) CWC occurrence data rescue	<i>“Dark Data”:</i> Large amounts of CWC data (video, distribution) are not available in open-access online databases. <i>Uncoordinated efforts:</i> Data rescue activities are fragmented and independent. <i>Analysis bottleneck:</i> Utility of video data is constrained by the time and human expertise needed for analysis.	<i>FAIR data:</i> Implement funding body support to facilitate uploading data as Findable, Accessible, Interoperable, and Reusable (FAIR). <i>Global coordination:</i> Promote Ocean Biodiversity Information System as a universal database and coordinate data/imagery standardization (e.g. SMaRTaR-ID and Fathomnet). <i>AI-assisted analysis:</i> Use open video catalogs to train Artificial Intelligence (AI) algorithms for automated data identification and rescue.
(6) Public knowledge and awareness	<i>“Hard Sell”:</i> The deep-sea is distant from public life and can conjure negative associations, leading to public apathy. <i>Lack of awareness:</i> Low public knowledge of CWC ecosystems.	<i>Targeted outreach:</i> Implement targeted community outreach and education to reverse public apathy. <i>Flagship species:</i> Use CWCs as “flagship and umbrella” species, leveraging their positive public appreciation (beauty, biodiversity habitat) to build political support.

conservation planning. In addition, the drivers of CWC habitat suitability for CWC are crucial to understand, as this knowledge will underpin current and future climate refuges (Morato et al. 2020), restoration efforts, and conservation.

It is also important to document historical CWC distributions from past periods of climate change and oceanographic rearrangement given the identified importance of dead CWC as habitat (e.g. Robinson et al. 2014; Fink et al. 2015; da Costa Portilho-Ramos et al. 2022; Vertino et al. 2019; de Carvalho Ferreira et al. 2022). Efforts to look at historic distributions have shown that some CWC reefs have been in situ for thousands to hundreds of thousands of years, pointing to long-term resilience. Similar to reefs, geochemical dating has shown that some

non-reef scleractinian corals have been in existence for more than a quarter of a million years (Robinson et al. 2007). In both cases, studies also show that the CWC ecosystems thrive and die over time, with likely drivers including food supply, larval transport, and environmental conditions. Such data inform our understanding of current coral distributions and allow us to investigate potential drivers of local extinctions and growth, informing management and restoration efforts.

**Prioritized Knowledge Gap 2: the Geographical Gaps of CWC Exploration.** CWCs are found globally, but there are still large geographical gaps in knowledge. This issue is not specific to CWCs, as only approximately 27.3% of the seafloor has been



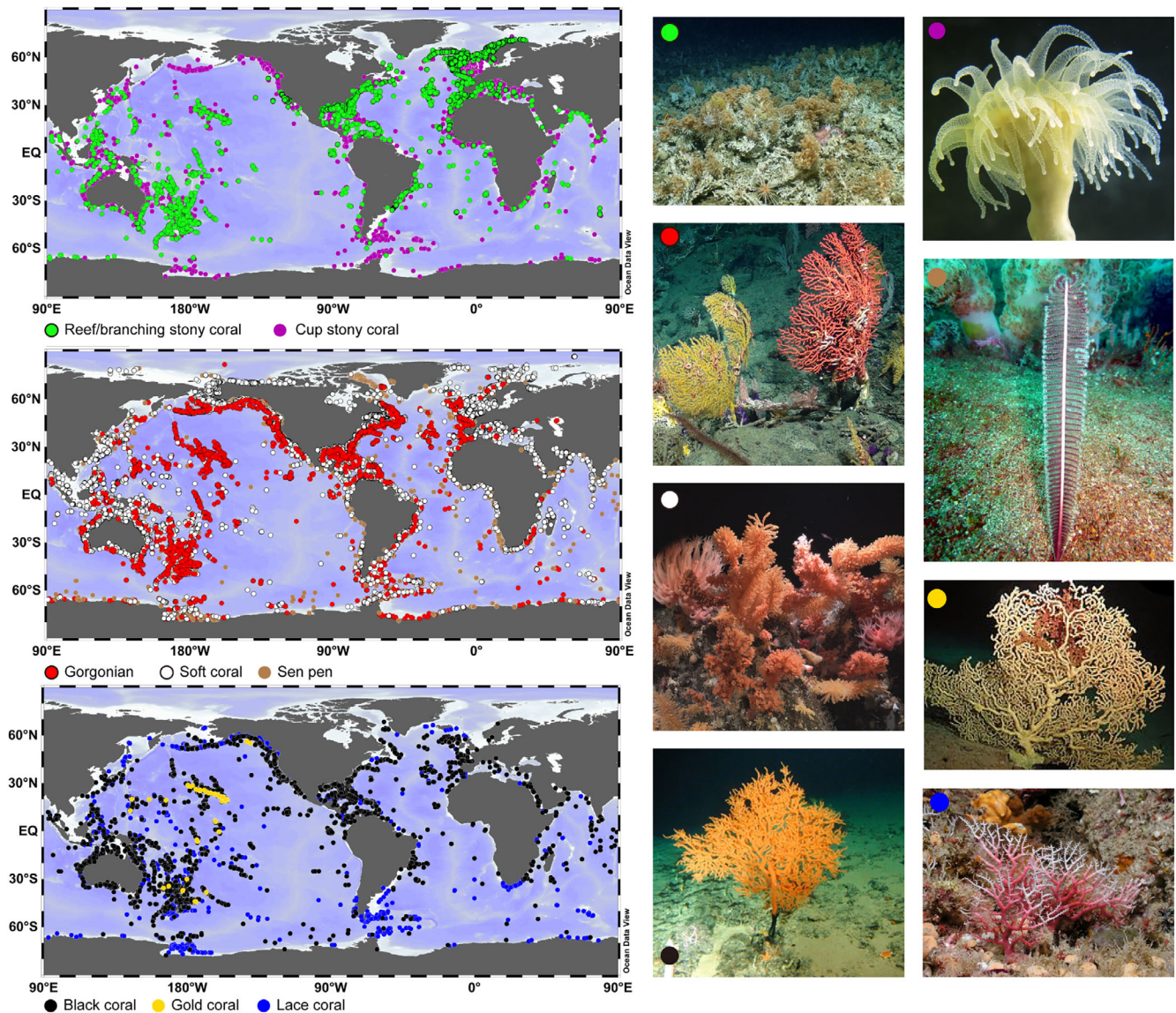


Figure 2. The distribution of CWC occurrence records from National Oceanic and Atmospheric Administration (NOAA), United Nations Environment Programme - World Conservation Monitoring Centre (UNEP-WCMC) (Freiwald et al. 2021) and (Cairns & Zibrowius 2013; Filander et al. 2021), with edits to remove erroneous points. “Stony coral” is Order Scleractinia. The green dots represent reef/branching stony coral WHOI, Woods Hole Oceanographic Institution; NSF, U.S. National Science Foundation; (photo credit: UBristol/WHOI/UESsex/UBoise/NERC/NSF/National Park Galapagos); the purple dots represent cup stony coral (photo credit: A. Gori) (Gori et al. 2016); “Gorgonian” represents Order Scleractinia (red dots, photo credit: L. Robinson) (Robinson 2014), except sea pen (Order Pennatulacea) (brown dots, photo credit: Gary C. Williams, California Academy of Sciences); “Soft coral” is Malacalcyonacea (white dots, photo credit: Schmidt Ocean Institute). “Black coral” is Order Antipatharia (black dots, photo credit: NOAA); “Gold coral” is *Kulamanamana haumeae* (yellow dots, photo credit: Sinniger et al. 2013); “Lace coral” is family Stylasteridae (blue dots, photo credit: D. Burdick).

mapped (GEBCO Bathymetric Compilation Group GBC 2025). The distribution of CWC reefs is wider than currently known due to the limited extent of ocean exploration efforts, and as mentioned above, data recording in international databases (Cordes et al. 2023). For example, the most abundant CWC occurrence records occur in the most frequently explored regions (Northeast Atlantic, United States continental margins, and Southwest Pacific; Fig. 2), which indicates a geographic bias in distribution data reflecting exploration effort. Such a bias could

significantly influence predictions of suitable CWC habitats. Based on current distribution data and model predictions (Cordes et al. 2023), geographic gaps in CWC research, areas ripe to investigate, include the west coast of Africa, parts of the western Indian Ocean (e.g. north of Madagascar, around the Seychelles, off the Horn of Africa, the southern shore of the Arabian Peninsula), the eastern Indian Ocean (e.g. Bay of Bengal and the Andaman Sea), large parts of the Pacific (e.g. Northwest Pacific, central and southern East Pacific),

as well as the Southern and Arctic Oceans. This exploration bias is most pronounced in the High Seas and ocean regions adjacent to Low- and Middle-Income Countries (LMICs) where access has historically been determined by capacity instead of shared scientific priority (Supplement S1). The United Nations High Seas Treaty (BBNJ) represents a pivotal shift, establishing a framework that promotes equitable capacity building and technology transfer to enable a more globally coordinated exploration of deep-ocean ecosystems. Understanding the global occurrence and diversity of CWCs in these High Seas areas will improve our understanding of CWC evolution, biogeography, and the drivers of their occurrence; all facets that will support successful conservation and, if appropriate, restoration efforts.

### CWC Community Composition and Maintenance

**Prioritized Knowledge Gap 3: Taxonomy to Inform Community Composition.** Different assemblages of CWC species form different habitats, especially in multi-species CWC gardens. Thus, it is hard to assess conservation value and restoration without accurate taxonomy. CWC exhibits extraordinary diversity, and many exhibit plasticity in morphological characters and few consistent characters across families, which complicates taxonomic identification (McFadden et al. 2022). Understanding CWC taxonomy is essential for conducting biodiversity, community, and species-specific studies. However, significant knowledge gaps and challenges persist in CWC taxonomy. Novel genomic techniques, in combination with morphological taxonomic studies (“integrative taxonomy”) (Padial et al. 2010), are challenging previous morphology-based taxonomies (McFadden et al. 2022; Morrissey et al. 2023). The most studied scleractinian species, *Lophelia pertusa*, has been synonymized into *Desmophyllum* genera and renamed *Desmophyllum pertusum* due to high genetic similarity and high skeletal plasticity between *D. pertusum* and *D. dianthus* (Addamo et al. 2016). In addition, there have been major revisions in Octocorallia systematics in recent years, with the number of recognized families increasing from 63 to 79 (McFadden et al. 2022). Similarly, the taxonomy of Stylasteridae has undergone substantial revisions (Cairns 1984; Cairns & Lindner 2011), albeit none so far with genome-wide next-generation sequencing data.

Even though a small but dedicated global community of morphological taxonomists focuses on identifying and curating the vast number of undescribed CWC species, their number remains limited, hindering advances in related studies, e.g. CWC biogeography, ecosystem biodiversity, and endemism. Similarly, CWC taxonomy is important in understanding species-specific interactions, such as symbioses, growth rates, and biomineralization, and thus resilience to environmental change and species-specific conservation status. Ultimately, the lack of adequate taxonomic information impedes the development of effective conservation as well, given some species are challenging to tell apart and thus “species” studies are sometimes (often) confounded. Considering the foundational role that taxonomy plays for the above-listed research, greater support for taxonomy is of utmost importance.

### CWC Early Life History

Reproduction is a fundamental ecological process inherent to the life cycle of all species, essential for sustaining population growth and expansion (Strömberg & Larsson 2017; Waller et al. 2023). Understanding the reproductive processes of CWCs is a crucial aspect of understanding resilience and natural recovery from impacts, as well as the development and implementation of effective conservation and restoration strategies. Although the number of CWC reproduction studies is increasing, to date they cover fewer than 4% of known CWC species (Waller et al. 2023). There are substantial knowledge gaps obscuring our understanding of CWC potential for recovery, and they pose significant challenges to conservation and restoration efforts. The workshop participants agreed on four significant knowledge gaps to CWC restoration and conservation, and we expand on them below here:

### Prioritized Knowledge Gap 4: Sexuality, Gametogenesis and Asexual Reproduction.

The sexuality patterns and gametogenesis processes of most CWC remain poorly understood. While gonochorism (coral individuals or colonies are male or female) is the predominant sexual strategy across examined taxa, instances of hermaphroditism (both sexes within a single colony) have been observed in Scleractinia and Octocorallia (reviewed in Waller et al. 2023). Some groups, like Stylasteridae, are poorly studied (Brooke & Stone 2007) (all were gonochoristic brooders), making definitive conclusions about sexual strategies for this group challenging. The details of gametogenesis, such as timing, maturation, periodicity, and how environmental factors affect these processes, are insufficiently documented in Stylasteridae, and even within the relatively well-studied Scleractinia, knowledge is still poor compared to shallow-water counterparts (Waller et al. 2023). Furthermore, data are lacking on asexual fragmentation and reproduction as a process of reef and community building. Although fragmentation in *D. pertusum* as a mechanism for reef growth has been reported (Wilson 1979), subsequent research on this topic has been notably sparse. The literature is limited to a few isolated studies on related processes, such as asexual budding (Waller et al. 2002) and polyp bailout (Rakka et al. 2019). Understanding these clonal processes is critical, as they represent a potentially dominant vector for CWC restoration, mirroring their importance in the restoration of shallow-water tropical corals.

### Prioritized Knowledge Gap 5: Sexual Maturity and Fecundity.

Age at sexual maturity and fecundity play pivotal roles in CWC population dynamics and, consequently, their capacity to recover from disturbance; however, very little detail is known for most species (Waller et al. 2023). Inconsistent measurement methodologies of maturity criteria and fecundity assessments in current research underscore the challenges of establishing generalized methods in this field; suggestions have been proposed in Waller et al. (2023). Moreover, research efforts have predominantly concentrated on well-documented taxa (e.g. Scleractinia and Octocorallia), with sexual maturity studies existing for only two species of Antipatharia and none



on Stylasteridae. In the context of the few studies available, Scleractinia exhibit the highest fecundity, while brooding Octocorallia exhibit the lowest (Waller et al. 2023). Species that produce large quantities of larvae may show higher connectivity between source and sink populations than those that produce fewer offspring since a greater number of offspring produced increases the chances of successful recruitment (Johnston & Larsson 2019). Like higher fecundity, early maturity may, but will not necessarily, result in larger quantities of larvae produced during a coral life span. How changing environmental studies and sublethal stress impact reproductive output is rarely studied. Knowledge about age of maturity is key for restoration purposes and, together with enhanced insights into CWC fecundity, can help estimate levels of fragility and resilience within CWC populations and holds the potential to develop more efficient management plans with conservation purposes and successful restoration strategies.

**Prioritized Knowledge Gap 6: Reproductive Mode and Seasonality.** When it comes to spawning time, knowledge about this is crucial in estimating connectivity among populations in, e.g. an MPA network using biophysical larval dispersal modeling. In a water basin, the circulation pattern and current velocities differ seasonally, so knowing which period of the year to run the model is important for species that display seasonality. Research so far has demonstrated that CWC exhibit either seasonal (reproductive activities happen during specific seasons or times of the year) or periodic (reproductive activities at regular intervals, not necessarily aligning with specific seasons) reproduction. In Scleractinia, about half of the examined species exhibited periodicity (Waller et al. 2023). Periodicity has also been observed in Octocorallia, with seasonality seen in some species too (Waller et al. 2023), but the few studies prevent broader statements about the proportion of each.

Direct observation of actual reproductive spawning or offspring release events is required for assessing reproductive mode (Waller et al. 2023). As viewing spawning is near impossible in deep waters, researchers more commonly rely on assessing stages of gamete development to infer the timing of maturation and egg release. An expansion of this knowledge in the CWC field is feasible and required.

Corals have two sexual reproductive modes or strategies, both found among CWC. For brooders, the fertilization of eggs occurs in or on the surface of maternal colonies, and larvae are fully developed before being released. Broadcast spawners, on the other hand, release gametes into the water column, where fertilization and embryonic and larval development take place. Scleractinian reef-forming CWC studied to date are all, with one exception, broadcast spawners, as are Antipatharia; stylasterids are brooders, whereas both reproductive modes are found among octocorals and solitary scleractinians (Johnston & Larsson 2019; Waller et al. 2023). The larvae of broadcast spawning corals generally have longer pelagic larval duration (PLD), resulting in higher potential to disperse widely outside their natal reef, whereas brooding corals release mature larvae directly that are ready to settle within much shorter periods

(Harrison & Wallace 1990). This implies that a site with brooding corals has great chances of being self-seeded, whereas a location with broadcast spawning corals might be largely, if not totally, dependent on larval input from surrounding populations for rejuvenation. Addressing this knowledge gap through further research on underexplored taxa is imperative for both restoration and management purposes.

Comprehensive understanding of reproductive patterns and timings can also enable better mapping of potential population connectivity and empower marine managers to establish well-connected self-sustaining MPA networks (prioritized knowledge gap 8), and to synchronize restoration initiatives with natural reproductive events, thereby enhancing the prospects of successful larval settlement and colony establishment for restoration.

**Prioritized Knowledge Gap 7: Fertilization, Larval Development, Behavior, and Settlement.** Our best understanding of CWC fertilization, larval development, behavior, and settlement is in the reef-forming Scleractinia and a small part of Octocorallia, with limited data available for sea pens (Pennatulioidea) and other CWC taxa. There are, to date, no published data on fertilization dynamics in CWC, although work on spermatozoa swimming, gamete longevity, and sperm concentration for optimal fertilization is ongoing for a few species, such as *D. pertusum*. For management and restoration purposes, such data can help to understand how fragmentation of habitats and density of restored individuals affect realized fertilization rates and thereby larval production.

The larval development rate and the swimming behavior of larvae affect dispersal potential. One important property is the pre-competency period, that is, the minimum amount of time after releasing that embryos and larvae spend in the water column before maturing enough to settle. As discussed above, brooding species release fully developed planulae, and in a recent study, they report the settlement of brooded larvae of *Goniocorella dumosa* after 2 days (Beaumont et al. 2024). In contrast, larvae of the broadcast-spawning *D. pertusum* are not competent to settle until, at the earliest, about 5 weeks of age (Strömberg & Larsson 2017). These larvae also display ontogenetic vertical migration with upwards-directed swimming during their first month. Such properties, together with embryonic and larval buoyancy and larval type (some brooded larvae only crawl), determine where in the water column embryos/larvae are transported during their different life phases. With both current direction and velocity normally varying with depth, vertical position will greatly influence the direction and distance larvae are transported.

Although settlement has been documented for some CWC species under laboratory conditions, and some preferences for substrates have been tested, no comprehensive studies about prerequisites for settlement, influential environmental factors, or important cues to settlement (which clearly link to population connectivity) have to date been undertaken. While microbial biofilms have been shown to be important to tropical coral larvae for settling (e.g. Turnlund et al. 2025), there has been no experimental evidence that they are important for CWC species.

Larvae were found to prefer biofilm conditioned surfaces in *G. dumosa*; however, larvae did successfully settle on a variety of substrates (Beaumont et al. 2024), and similar results have been seen in the cold-water octocoral *Driftia* sp. (Sun et al. 2010). This is a fundamental knowledge gap when it comes to understanding natural recovery from damage or planning restoration, e.g. when offering artificial reef structures for spontaneous settlement of larvae.

#### CWC Metapopulation Dynamics and Connectivity

**Prioritized Knowledge Gap 8: Connectivity of CWC Populations and Population Structure.** Ecological spatial connectivity refers to the flow of genes, propagules, and individuals among spatially distinct populations. To ensure the recruitment of restored sites and the resilience of restored populations, it is essential to study CWC population connectivity. Well-connected populations are more resilient to anthropogenic disturbance, as larvae from source populations can help passively restore damaged sites by recruiting to suitable habitats (Jenkins & Stevens 2018). Genetic studies are a principal method for estimating marine population connectivity; however, the difficulty of obtaining large numbers of CWC specimens has contributed to a critical knowledge gap in the understanding of CWC genetic connectivity, with only a few studies available (Morrison et al. 2017; Taylor & Roterman 2017). Additionally, often CWC specimens have historically been preserved in formalin—a chemical that preserves tissue well for histology but destroys DNA. Recently, the increased availability of cheaper next-generation sequencing has increased the focus on CWC specimens, including some preserved in formalin, helping to promote more extensive in-depth genetic population connectivity studies using hundreds to thousands of DNA markers (e.g. Erickson et al. 2021). Such studies have generally focused on local to regional connectivity—the scales that are most relevant for conservation and restoration—but are few in number. Similar broad-scale studies using these and other methods can also elucidate the connectivity of CWC across and potentially among ocean basins to understand CWC evolutionary patterns and potential responses to climate change.

A complementary approach to genomic population connectivity is to estimate potential connectivity using ocean circulation models in combination with particle tracking. North Atlantic larvae were found to potentially disperse great distances, depending on larval behaviors and durations (Gary et al. 2020), while another recent study suggested that differences in connectivity can arise from seasonal differences in reproduction (Metaxas et al. 2019). These methods rely upon well-suited oceanographic models which are largely limited by sub-surface oceanographic velocity monitoring gaps and can be hard to identify (Ross et al. 2020).

Coral connectivity is reliant on currents that will carry larvae to a suitable settlement location; however, as discussed above, very little is known about CWC reproduction and larval behavior. Several environmental factors may constrain larvae, such as differences in water temperature, salinity, oxygenation, nutrient

availability, and barrier currents (e.g. Quattrini et al. 2015). Understanding these connectivity barriers and the gene flow between CWC populations can better inform management of these VMEs and ensure there are recruits to repopulate disturbed areas and perpetuate existing patches (Jenkins & Stevens 2018).

#### CWC Growth Rates and Resilience to Change

**Prioritized Knowledge Gap 9: Growth Rates and Biomineralization of CWC and Potential Impact Factors.** CWC biomineralization strategies and growth rates comprise a critical knowledge gap for informing the development of CWC conservation and restoration approaches. Growth varies considerably among CWC; they are generally slow-growing and long-lived—characteristics that contribute to their vulnerability and slow expected recovery from damage. Currently, three primary methodologies are employed for determining CWC growth: in situ and ex situ observations, and geochemical dating (e.g. growth band counting and bomb  $^{14}\text{C}$  dating). Each method poses challenges. First, detection of in situ growth requires prolonged observations as growth rates of CWC are generally slow, even for species considered to be fast-growing (Orejas et al. 2008); it is a rare endeavor to visit deep-sea locations twice to observe growth. Precise measurement of growth increments is also challenging for in situ studies. Although ever-improving three-dimensional photogrammetry can measure in situ growth (Bennecke et al. 2016), available growth data remain limited and predominantly focus on fast-growing species.

Ex situ (aquaria) growth rate studies can give precise growth measurements, but do not represent the complexity of in situ conditions. Also, CWC maintained in aquaria is often over-fed and preserved from environmental disturbances, which often lead to an overestimation of their growth rates. Using geochemical dating to measure the age of coral skeletons offers an alternative to estimate average growth rates (Sabatier et al. 2012). Growth rates derived from geochemical dating represent long-term (decadal) averages and are not well-suited to capturing variations in CWC growth attributable to short-term environmental fluctuations (Liu et al. 2023). These challenges underscore the complexity of assessing CWC growth rates, especially considering species-specific differences.

CWC skeletons provide support for coral polyps and contribute to complex three-dimensional habitat formation (Buhl-Mortensen et al. 2010). Most CWC skeletons are calcium carbonate (Scleractinia, Octocorallia, and Stylasteridae) and are deposited in one of two possible mineral crystalline structures: aragonite or calcite (Roberts et al. 2009; Robinson et al. 2014), or proteinaceous organic matter (Antipatharia, gold coral, and some Octocorallia). In principle, as observed in shallow symbiotic corals, the formation of inorganic aragonite and calcite demands carbonate supersaturation. However, many CWC can build their skeletons even in undersaturated seawater (Stewart et al. 2022) by modulating their internal calcifying fluid (Adkins et al. 2003) or without modulating this fluid, as in Stylasteridae (Stewart et al. 2022), and through alternative strategies, such as protective organic templates and/or



coatings (Gabay et al. 2014). However, apart from these hints, the exact mechanisms through which CWC build their skeletons remain largely unknown (Stewart et al. 2022). The complicated biological modulation of skeletal growth in CWC different species impedes our understanding of the controls on CWC growth, and therefore the development of effective active restoration strategies.

Comprehensive insights into growth patterns and key determinants governing CWC morphological development, particularly during juvenile stages, are lacking (Corbera et al. 2022). Factors known to play a role include regional hydrodynamics (Corbera et al. 2022), food availability (Larsson et al. 2013), biomineralization (Stewart et al. 2022), seawater chemistry (e.g. oxygen and carbonate saturation) (Ross et al. 2020), and temperature (da Costa Portilho-Ramos et al. 2022). Yet, despite our overarching understanding of these controlling factors, few data are available regarding how these factors influence CWC growth (Corbera et al. 2022). Consequently, there is an imperative for research concerning factors controlling CWC growth patterns and rates, perhaps with particular attention directed toward underexplored taxa, such as Stylasteridae.

#### Prioritized Knowledge Gap 10: the Food Dynamics of CWC.

A comprehensive understanding of food/ nutritional dynamics is needed to identify optimal conditions for CWC conservation and restoration. Specific priorities include the description of the quality and quantity of food available in the close surroundings of CWC corals, feeding mechanisms, preferred food sources, and seasonal variability, as CWC are believed to rely on carbon input from the ocean surface (Goldberg 2018; Girard et al. 2022) or below when there is a deep chlorophyll maximum layer (Liu et al. 2023). Depending on species or habitat, their food sources may include phytoplankton, zooplankton, fecal pellets, suspended particulate organic matter (POM), or bacteria (Dodds et al. 2009; Mueller et al. 2014; Salvo et al. 2018). *Desmophyllum pertusum* is the most studied species and is found to be opportunistic, feeding on various organic food sources with a preference for zooplankton (Dodds et al. 2009; Mueller et al. 2014). However, fatty acid and lipid profiles suggest CWC have some selective feeding associated with taxonomy (Salvo et al. 2018). For example, *D. dianthus* and *Madrepora oculata* in the Mediterranean Sea consume mainly living zooplankton, rather than suspended POM (Naumann et al. 2015). In addition to Scleractinia, studies suggest zooplankton might also be the main food source of Octocorallia (Rakka et al. 2021; Liu et al. 2023) and Antipatharia (Rakka et al. 2020). However, there are also studies suggesting fecal pellets are dominant diet contributors of Octocorallia (Pugsley et al. 2025). Results appear to be taxa specific. A sufficient understanding of CWC food sources is overall lacking.

There is little information on CWC feeding mechanisms. Scleractinia employ mostly tentacle capture, likely involving nematocysts, mucociliary activity, and/or extracoelenteric digestion, but may also use mucus nets (Murray et al. 2019), and the relative contribution of each process has not been evaluated (Goldberg 2018). For Octocorallia, tentacular filtration

of weakly swimming mesozooplankton, particulates, and pico-plankton is thought to be their main feeding mechanisms (Lewis 1982). Octocorallia are also thought to be opportunistic feeders and shift their diet according to season (Orejas et al. 2003).

CWC morphology, growth, and, importantly, orientation to currents are additional factors related to feeding success (Buhl-Mortensen & Mortensen 2005). Orientation specifically has been noted as a potentially important factor for restoration, that is, orientation of transplanted colonies to currents can be crucial for survival (Ross et al. 2025). Generally, the feeding biology for the majority of CWC is not clear. In addition, a better understanding would also inform implications for CWC of predicted changes in sea surface productivity with climate change (Jones et al. 2014).

#### Recommendations

The above priorities aim to bridge critical gaps in knowledge required for transformative advances in effective conservation and restoration of CWC in the next 10 years. Some overarching recommendations to researchers, managers, and donors are highlighted below:

- (1) Fostering a collaborative and open research ecosystem
  - We encourage all actors in the CWC field to focus on widening participation in CWC research, conservation, and management to ensure its equitable future, and to collaborate to both build collaborations, knowledge exchange, and capacity to fill geographical gaps in CWC knowledge.
  - To move beyond the slow pace of academic publication, we encourage establishing and supporting expert networks that promote the rapid exchange of ideas, results, and methods. Therefore, we recommend that funding agencies actively foster this collaboration by prioritizing proposals that include well-defined plans for international networking and knowledge exchange.
  - We strongly recommend a coordinated effort to integrate existing CWC location data into existing open-access platforms, such as the Ocean Biodiversity Information System (<https://obis.org/>), thereby supporting the global accessibility and understanding of biogeography, ranges, diversity, and conservation status. Additionally, we encourage submission of identified genetic sub-samples to national/regional curated collections and the placement of genetic data into open-access online platforms. Such specimens could be accumulated to have enough for population genomic research, as well as important evolutionary studies. This knowledge is a necessary underpinning of current and future conservation and restoration efforts.
- (2) Translating science into protective policy and management
  - We recommend active participation by the CWC scientific community in relevant policy forums, such as the Conference of Parties of the United Nations Framework

Convention on Climate Change (UNFCCC) and the Convention on Biological Diversity (CBD), where CWC has not been a particular focus of events and discussions. We also recommend the exploration of innovative endeavors that bring together science, technology, indigenous knowledge, policy, and the arts, as this breadth of experience and knowledge is required to approach this challenging task.

- Immediate protection should be granted to currently undisturbed (i.e. untrawled) CWC habitats. These areas represent potential refugia, sources of larvae for connected populations and restoration, and scientific reference sites. Management plans should also enforce a transition to less-damaging fishing gear in adjacent areas.
- (3) Reimagining funding for long-term success
- CWC conservation and restoration can be advanced by focusing efforts on understanding CWC taxonomy, reproduction, growth, and feeding. This basic understanding of CWC biology is required to formulate successful conservation and restoration efforts and must be prioritized in funding schemes.
  - Critically, the short-term (approximately 3–5 years) nature of typical grant cycles is fundamentally misaligned with the decades to centuries recovery of CWC. We urge funding bodies and donors to pioneer innovative, long-term funding models.

The above recommendations span many fields of research, management, and politics relevant to CWC conservation. A broad community of CWC practitioners will be involved in addressing these recommendations, ensuring that knowledge gaps concerning CWC ecosystems are filled in order to support current and future CWC conservation and restoration priorities. Improved understanding of CWC will not only support their conservation and restoration, but also that of the ecosystems they sustain and coral-like species, such as cold-water sponges. Considering the expanding threat of human activities to CWC systems, their century-scale recovery times from disturbance, and the current lack of knowledge concerning many aspects of these ecosystems, the research priorities outlined here are considered urgent to ensure the long-term survival of these essential ocean habitats.

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## Conflict of Interest Statement

The authors declare that they have no competing interests.

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## Supporting Information

The following information may be found in the online version of this article:

**Supplement S1.** Overarching priorities and challenges for CWC research and conservation.

**Supplement S2.** Cold-water coral distribution.

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