Global Biodiversity in Cold-Water Coral Reef Ecosystems

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Lea-Anne Henry and J. Murray Roberts

Abstract

Over half of all scleractinian coral species inhabit ocean depths greater than 50 m, some of which are capable of constructing reefs tens of kilometers long and hundreds of meters high. The biodiversity of life found on these cold-water coral reefs is astounding yet remarkable since, in contrast to the photic and mesophotic zones, so few coral species actually create a framework matrix at these depths. In light of rapid climate change and unprecedented rates of anthropogenic disturbance, it is urgent we understand how biodiversity in the depths of our oceans is coupled to the persistence of these habitats. We provide a synthetic overview of animal biodiversity associated with major reef framework-forming species, discussing this with respect to global trends in species diversity, composition, and regional species pools, large knowledge gaps, and also the frontiers in technology that cold-water coral science is adopting to help address these gaps.

Keywords

Cold-water coral reefs • Sharks • Fauna • Species diversity • Community assembly • Biogeography • Taxonomy • Landers • Underwater observatories • Robotics • Genomics

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1.1 Introduction

Earth's vast deep oceans covering over two thirds of the planet are home to aphotic cold-water coral (CWC) reef ecosystems. Although less familiar to the public than shallow warm-water corals, CWC reefs are not only more globally distributed across wider latitudinal ranges than their tropical counterparts but they also harbor an equally remarkable level of biological diversity as that found in tropical reefs (see ▶ Chap. 2, "Caribbean Coral Reefs: Past, Present, and Insights into the Future" by Jordán-Dahlgren and Reyes-Bonilla in this volume). For example, 35 species of benthic Hydrozoa (hydroids) were recorded from CWC reefs in the southeastern USA, compared to 43 from tropical reefs off Belize and only 11 from Bermuda coral reefs (Henry et al. 2008). From bacteria to fungi, single-celled animals to large vertebrates such as sharks, this remarkable variety of life is the product of the sheer physical complexity of CWC reefs, their underlying seafloor topography, and interactions with water currents. These physical mechanisms supply high quality food to reef organisms, fuel the food chain, and promote species interactions, all of which contribute to the globally rich diversity harbored by these deep ecosystems.

At last count, there are overall 711 known recent azooxanthellate scleractinian species but only six major reef framework-building species (Roberts et al. 2009;

Roberts and Cairns 2014). These include: *Oculina varicosa*, *Madrepora oculata*, *Lophelia pertusa*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia profunda,* and *Bathelia candida. Enallopsammia rostrata* can also occur in very high densities. Although most of these reef builders are globally cosmopolitan, each occurs within its own particular environmental niche defined by the coral's biological, physical, and geochemical requirements (Flögel et al. 2014).

Over several millennia, coral colonization, recruitment, and growth processes are shaped by successional geochemical cycles of cementing, sediment baffling, and erosion. These processes can engineer giant coral carbonate mounds hundreds of meters high, structures which have in some cases persisted for over three million years (Raddatz et al. 2011).

Their habitat heterogeneity and associated high biological diversity, including valuable fish stocks, have attracted large-scale exploration and mapping initiatives, primarily by petroleum and fishing industries, governments, and academia, to characterize coral carbonate mound geology and biology. This has led to many new insights into how CWC reefs create and maintain species (α) and community (β) diversity, but also how they contribute to the wider regional biodiversity (γ) in our seas. Several paradigms of CWC reef biodiversity emerge from studies around the globe but many more knowledge gaps remain. While the most serious gaps can be addressed simply by continued exploration, technological frontiers can overcome some limitations to help acknowledge what stands to be gained by halting the global degradation of CWC reefs and conserving these fragile ecosystems.

2 Biodiversity Associated with CWC Reefs

Beyond the primary producers of the photic zone, the richness and functional diversity of species that inhabit CWC reefs clearly demonstrate that these ecosystems, and the complex substrata they provide, support a great diversity of trophic levels in the benthic food web (see ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems" by Buhl-Mortensen et al. this volume) with important roles in regional biogeochemical cycles (van Oevelen et al. 2009; Cathalot et al. 2015; Rovelli et al. 2015). Based on the ways in which this fauna use the coral habitat to live and feed, this functional diversity can be separated into categories that may overlap in the types of species they attract. The smaller, almost microscopic, biofilm organisms (see Sect. 2.1) are attracted to the bacterial and fungal mats along with particles that have encrusted coral surfaces. Fauna also include grazers, deposit feeders, and small benthic predators that find niches among reef polyps, branches, and other microhabitats (see Sect. 2.2). Hard larger coral surfaces are colonized by a diverse range of larger sessile suspension and filter-feeding epifauna (see Sect. 2.3). Benthopelagic and benthic demersal fish communities (see Sect. 2.4) also visit the reefs to forage, find refuge, and breed.

2.1 Fauna Associated with Coral Biofilm, Including Meiofauna

Small sponges, calcareous tube-building polychaetes, hydroids, and bryozoans encrust areas between coral branches and polyps and host a mixed assemblage of meiofaunal and smaller macrobenthic fauna including harpacticoid copepods, epifaunal nematodes, polychaetes, and platyhelminthes. The fauna associated with coral biofilm forms a very mixed and diverse animal community. In areas where CWC reef meiofauna and macrofaunal studies have been particularly intense such as in the northeast Atlantic and Mediterranean, species richness and changes in species composition over space (species turnover) at bathyal depths are in large part due to sediment accumulation around the corals themselves or just between coral polyps and branches that attracts a diverse mixture of both epifaunal and infaunal taxa including meiofauna (Raes and Vanreusel 2006; Bongiorni et al. 2010; Gheerardyn et al. 2010). Coral biofilm associated communities go on to support other CWC reef organisms, principally as food sources for brachyuran crabs, gastropods, polychaetes, urchins and seastars, and a variety of omnivores and predators (van Oevelen et al. 2009) including those that shelter amongst the biofilm-associated community (Fig. 1a).

2.2 Macrobenthic Grazers, Deposit Feeders, and Predators

The sediment-filled interstitial cavities found between coral polyps and branches also provide niches for a variety of larger sessile and mobile macrofauna that graze, settle between, or hunt for prey. These include bioeroding encrusting fauna such as bryozoans and sponges that excavate large cavities in the skeletons of live and recently dead coral in both deep-sea and coastal inshore CWC reefs (Beuck et al. 2007; van Soest and Beglinger 2009). The sponge family Clionaidae is particularly well known for the bioeroding capabilities of its constituent species on CWC reefs. Most of these species are endolithic living almost entirely within the coral skeleton, or grow to some extent outside the skeleton as well. The roles that CWC reef bioeroders play in these ecosystems cannot be underestimated, with growing concerns about ocean acidification increasing chemical bioerosion resulting in the coral reef framework essentially being dissolved before it has chance to build up into a geologically persistent reef (Wisshak et al. 2014). Deposit-feeders are most diverse in the coral rubble zone (Mortensen and Fosså 2006) or in adjacent noncoral areas (Henry and Roberts 2007). However, deposit-feeding nematodes can inhabit sediments in living coral habitat, with predominantly selective deposit feeders being present such as bacterivorous nematodes, but also with some nonselective deposit-feeding taxa (Bongiorni et al. 2010).

The abundance and biologically rich variety of small mobile prey among coral framework and rubble also make these habitats an excellent hunting ground for benthic predators such as carnivorous solenogaster molluscs, polychaetes (Fig. 1b), crustaceans, and echinoids, which themselves play hosts for other fauna such as

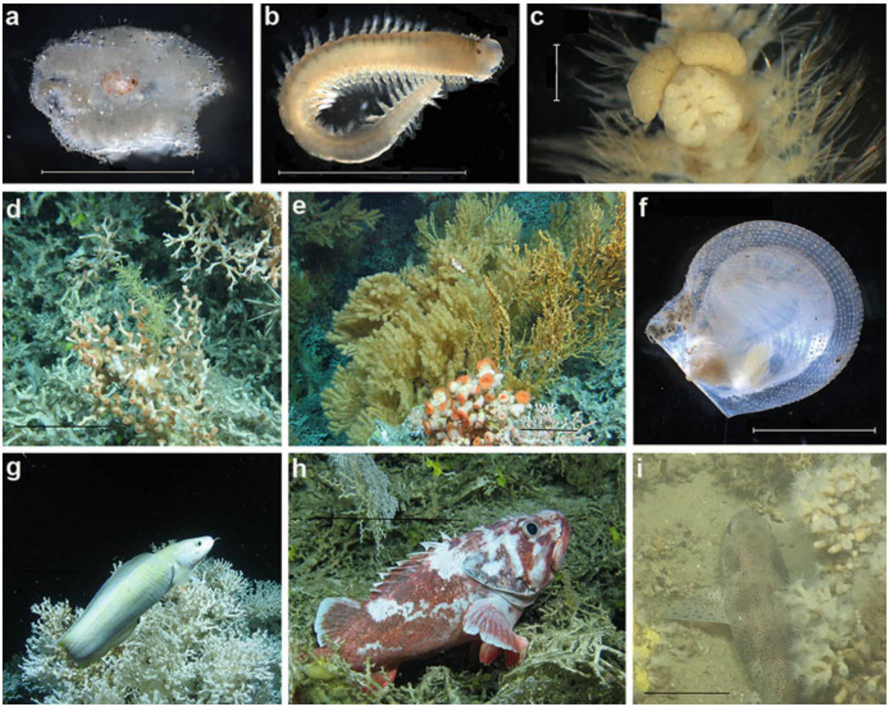

Fig. 1 Animal biodiversity associated with cold-water coral reefs is very high, as demonstrated by these images from northeast Atlantic *Lophelia pertusa* and *Madrepora oculata* reefs. The fauna associated with coral biofilm includes encrusting sponges in which the isopod *Caecognathia abyssorum* seeks refuge (**a**, scale bar 5 mm, water depth 857 m). Small carnivorous invertebrates like the polychaete *Nereimyra punctata* hunt among the coral biofilm and reef frameworks (**b**, scale bar 5 mm, water depth 857 m), while parasitic copepods find a host on a polynoid polychaete (**c**, scale bar 500 μm, water depth 857). Sessile suspension and filter-feeding epifauna like hydroids (**d**, scale bar 10 cm), gorgonian octocorals, and zoanthids (**e**, scale bar 10 cm, water depth approximately 700 m) and the bivalve *Delectopecten vitreus* (**f**, scale bar 5 mm, water depth 857 m) densely colonize the reef framework. Demersal fish such as the tusk *Brosme brosme* (**g**, scale bar 10 cm, water depth approximately 700 m) and the blackbelly rosefish *Helicolenus dactylopterus* (**h**, scale bar 10 cm, water depth approximately 700 m) hunt and rest among living and dead reef framework, as does the catshark *Scyliorhinus canicula* (**i**, scale bar 10 cm, water depth approximately 140 m) (All images taken by the authors; images **d**, **e**, **g**, **h**, and **i** were taken during the 2012 Changing Ocean Expedition (RRS *James Cook* cruise 073)

parasitic copepods (Fig. 1c). Urchins are known to aggregate in large numbers on CWC reefs to ingest live corals and coral skeleton and even shift their habitat use to the interior or base of coral skeletons in the presence of predators such as fish and decapods (Stevenson et al. 2014). Interestingly, CWC reefs in the southwest Atlantic have also been found to support a highly specialized group of carnivorous cladorhizid sponges (Lopes and Hajdu 2014). Their “sit and wait” approach to predation is associated with an entire loss of the classic sponge body plan of an aquiferous system or choanocyte chamber, and instead these sponges feed on crustacean prey.

2.3 Suspension and Filter Feeders

Some of the most biologically diverse components of the CWC reef ecosystem to colonize the stable reef framework are the suspension and filter-feeding fauna (Henry and Roberts 2007), typically comprised of sponges, cnidarians (hydroids and hydrocorals as in Fig. 1d, scleractinians, antipatharians, octocorals, and zoanthids as in Fig. 1e, anemones, benthic scyphozoans), bivalves (Fig. 1f), brachiopods, polychaetes, bivalves, bryozoans, crinoids, and tunicates.

The occurrence of these taxa in CWC reefs is directly related to the quality, availability, and retention capacity of food particles delivered to the reef by local hydrodynamics, without which, these sessile benthic animals could not survive. Local hydrodynamics are modified by seabed topography, an interaction that helps determine how suspension and filter-feeding communities are distributed over the coral reef, depending on which species can inhabit, e.g., stronger currents near the top of a mound versus slower currents in a seabed depression (Henry et al. 2013a).

2.4 Demersal Fish Communities

Demersal fishes most commonly observed on CWC reefs can be broadly divided into those with a very close association with the seafloor (benthic demersal) and those that swim more freely over the ocean floor (benthopelagic). Associations between CWC reefs and demersal fish are highly dependent on the spatial scale of the habitat, as well as fish species' niches and ontogeny (Biber et al. 2013; Kutti et al. 2014). This has made it difficult to discern clear patterns, but there is evidence that many teleosts and elasmobranchs appear to associate with reef habitats in different capacities such as foraging, finding refuge, and reproducing, and there is evidence for strong temporal, possibly seasonal, aspects to CWC reef habitat use by fish (Lavaleye et al. 2015; Ross et al. 2015). The overall result is that a number of fish species and increased fish densities tend to co-occur in areas with higher coverage of corals and biogenic substrata (Purser et al. 2013b). However, there may be local and regional differences in the ways in which fish make these associations. For example, although fish abundance was higher in coral areas than noncoral areas in the Arctic, Atlantic, and in the Mediterranean Sea, trends in fish diversity differed across areas, with only specific fish species being associated with corals in the Mediterranean and Arctic as opposed to the Atlantic where overall fish diversity was higher (Linley et al. 2015).

For example, commercially important demersal stocks of ling, tusk, and redfish (*Molva molva*, *Brosme brosme* seen in Fig. 1g, and *Sebastes marinus*, respectively) in the northeast Atlantic are all found in greater abundance in CWC reef habitats, with ling and tusk likely foraging on enhanced densities of benthopelagic fish and benthic crustaceans attracted to these structurally complex habitats (Husebø et al. 2002). For example, the average catch of redfish (*Sebastes marinus*) off southwestern Norway was 5.7 fish per long-line in coral habitats versus 0.8 fish in areas without corals (Husebø et al. 2002). Similarly, commercially important demersal blackspot seabream (*Pagellus bogaraveo*) and wreckfish (*Polyprion americanus*) in the Mediterranean Sea, as well as bycatch species such as conger eel (*Conger conger*) and blackbelly rosefish (*Helicolenus dactylopterus*, Fig. 1h), are all found in more abundance in CWC habitats. For example, the average number of blackbelly rosefish found in coral megahabitats of the Santa Maria di Leuca province in the Mediterranean Sea was 23.11 versus only 10.44 in noncoral habitats (D'Onghia et al. 2012). These positive associations with CWC reef habitats seemed to relate to enhanced foraging opportunities associated with the reefs (D'Onghia et al. 2010, 2012).

Juvenile size classes of many fish are also more abundant on CWC reefs than they are elsewhere, including the blackmouth catshark (*Galeus melastomus*) and the velvetbelly lantern shark *Etmopterus spinax* (D'Onghia et al. 2010, 2012). Increased numbers of conger eels (*Conger conger* and *Conger oceanicus*) that can be observed burrowing near the bases of coral reef framework in these habitats suggest a role for the coral ecosystems as refuges or resting areas as observed in the lesser-spotted catshark (*Scyliorhinus canicula*) among the reefs as seen in Fig. 1i (Henry et al. 2013b).

It is also emerging that globally, CWC reefs provide spawning habitat for oviparous (egg-laying) fish including deep-sea demersal elasmobranchs such as the blackmouth catshark (*Galeus melastomus*) and the Pluto skate (Quattrini et al. 2009; Henry et al. 2013b), among others being reported during exploratory ROV surveys (Henry et al. 2014b).

3 Emerging Ecological Paradigms

CWC reefs create and maintain very high levels of biodiversity compared to the surrounding seafloor (Henry and Roberts 2007). The occurrence of the CWCs themselves is a product of the right combination of oceanography (broadly referring to water mass structure and properties), hydrography (broadly referring to ocean mixing/stratification processes, ocean fronts, and hydrographic features such as internal tides, Taylor columns, and domes), geology (sedimentology and geomorphic features such as ridges, canyons, seamounts), and bathymetry that provide ideal conditions for the major framework-forming species.

These interactions and the sheer physical complexity of reef framework-forming corals allow CWC reefs to support the broad range of animals outlined in Section 2, as well as very high numbers of species per unit volume. Additionally, the life cycle of the coral structure itself from the very first colonizing polyp through to coral colony death actually creates a distinct zonation of CWC macrohabitats, similar to the vertical zonation patterns observed in other habitats such as intertidal rocky shores and shallow-water coral reefs in the photic zone. CWC macrohabitats typically grade from a background of primarily small coral sediments and fragments to larger pieces of coral rubble, followed by thick sediment-clogged dead coral matrix to a mixture of dead and live corals, which are then topped at the surface by living corals provided that recruitment of new corals continues.

Clear zonation patterns in the numbers of species and how these are equitably distributed (α diversity) across the different macrohabitat types are frequently evident, as are trends in the species composition (β diversity). The concepts of CWC reefs as biodiversity as well as nutrient cycling hotpots are rapidly emerging, effects that will have larger scale implications for regional (γ diversity) patterns in the deep sea.

3.1 Species (α) Diversity

A main driver of species diversity on CWC reefs is simply the physical zonation and stability of the different reef macrohabitats. This typically results in enhanced species richness on CWC reefs than off, a paradigm observed on the *Solenosmilia variabilis* reefs of the southwest Pacific (Thresher et al. 2014) and the *Lophelia pertusa*/*Madrepora oculata* reefs northeast Atlantic (Henry and Roberts 2007). Larger pieces of dead coral that no longer contain any live polyp-clearing parts are likely to offer reef fauna, particularly smaller ones, a high variety of niches with high physical stability. In fact, one of the most speciose CWC macrohabitats is the coral degradation zone, where larger fragments of dead coral and rubble are most abundant and living coral cover is sparse (Mortensen and Fosså 2006; Raes and Vanreusel 2006). This is in contrast to large but living sections of reef framework, which tend to be colonized (if at all) by specialists such as the excavating foraminifera *Hyrrokin sarcophaga* and the predatory polychaete *Eunice norvegica* (Mortensen and Fosså 2006) in the case of Norwegian *Lophelia* reefs, and the possible obligate specialist snail *Coralliophila* sp. in the case of *Lophelia* reefs in the Gulf of Mexico (Cordes et al. 2008). Smaller, finer-grained pieces of coral rubble and background sediments tend to have lowest species diversity (Mortensen and Fosså 2006). These observations suggest that substratum stability and low risk of mortality from coral polyps offer reef fauna the best chances at species coexistence.

Another main driver of α diversity in CWC reefs is the combined effects of oceanography and hydrography. Although not as well studied as effects of macrohabitat, CWC reef biodiversity appears to be higher in zones where two water masses interface (Henry et al. 2014b). This could occur either because fauna from two biogeographically distinct regions can now coexist, and/or because there may be enhanced tidal mixing associated with this stratification and internal tides, a biophysical effect that would result in increased particle delivery to reef fauna (Henry et al. 2014b).

3.2 Community (β) Diversity

Each CWC reef macrohabitat supports its own biological community, which in some cases, substantially differs from other macrohabitats and the adjacent surrounding seafloor habitats (Henry and Roberts 2007). This zonation is a product of gradients in substrata ranging from the surfaces of living and dead corals to the flatter aprons of smaller finer-grained pieces of dead coral rubble and underlying sediments. Zonation in these habitats is also a product of the fine and local scale differences in the hydrography. When the depth gradient is large enough, it can also be due to differences in the chemical oceanography of the waters bathing the corals (Thresher et al. 2014; Henry et al. 2014b), which can even produce zonation in the reef-building coral species themselves (Thresher et al. 2014). Importantly and less often considered are the effects of species ecology (Henry and Roberts 2007; Henry et al. 2013a), including life history traits, dispersal potential, environmental niches, and interspecific interactions including predation and competition.

Zonation also occurs across different CWC reef-building species in the same area. For example, the CWC reef megafaunal communities off southern Tasmania differed between live *Enallopsammia* corals (high megafaunal species richness, but low abundance), the live *Solenosmilia* corals (high richness, and high abundance), and the dead *Solenosmilia* and rock/rubble zone (low richness, with scattered megabenthos and encrusting fauna).

CWC reef zonation across macrohabitats is well documented. Globally, there are fewer species associated with macrohabitats having 100% live coral cover, with the exception of large mobile decapods, some echinoids, crinoids, and demersal fish, a relationship that is often seen in shallow water coral reefs of the photic zone. This probably relates to the fact that these kinds of large stable habitat offer these specific animals opportunities to rest, forage, find refuge, and hunt.

The most biologically diverse part of the CWC reef is actually the coral degradation zone, which grades from the dead/live coral framework (Fig. 2) to the coral rubble apron, a transition that can be quite distinct (Fig. 3). Here, many sessile epifaunal species that need strong currents and stable substratum may coexist, and often their reproductive and dispersal habits are such that very dense aggregations of these animals form extensive patches of, e.g., some sponges, zoanthids, cup corals, hydroids, brachiopods, bryozoans, and large sabellid and serpulid polychaetes (Henry et al. 2013a). Living amongst these will be specialist predators such as nudibranchs, hesionid polychaetes, caprellid amphipods, and carnivorous sponges, capable of feeding on the rich sessile epifauna and benthopelagic zooplankton. Mobile megafauna also inhabit this zone, such as the decapod crabs *Munidopsis* spp. and *Eumida picta* in the case of *Lophelia* reefs in the Gulf of Mexico (Lessard-Pilon et al. 2010). There is also a rich endofauna living inside dead coral skeletons including excavating macroboring fauna such as sponges, bivalves, polychaetes, and sipunculids. Smaller finer-grained pieces of coral rubble are typically colonized by only the most opportunistic and ephemeral species of groups like hydroids, bryozoans, and

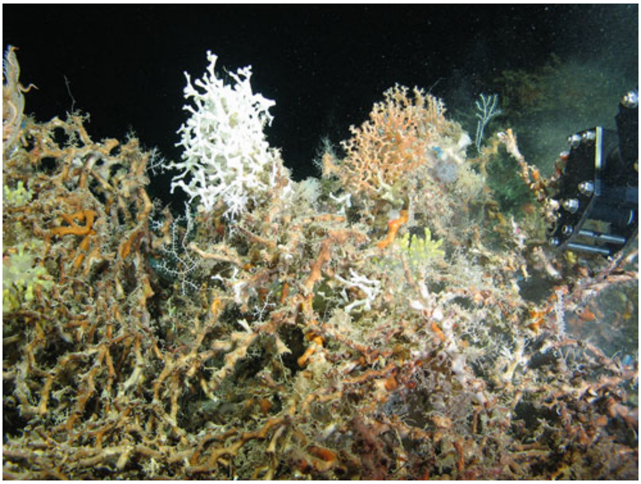

Fig. 2 ROV images showing part of a mixed *Enallopsammia rostrata*/*Lophelia pertusa* reef on the western slope of the Great Bahamas Bank. Dense and highly diverse epifaunal assemblages are seen inhabiting the mixture of live and dead coral framework in waters approximately 600–700 m deep (Images copyright MARUM, University of Bremen/Germany)

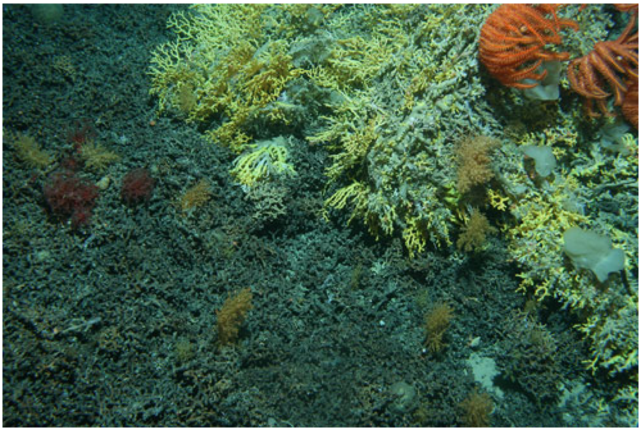

Fig. 3 The biologically rich live/dead coral degradation zone may include sharp transitions into dead coral fragments, as exhibited by these thickets of live reef-forming branching stony coral *Enallopsammia rostrata* (*yellow* color morph) at a depth of 912 m on the seamount Diabolical in the Graveyard Knoll area, Chatham Rise, southeast New Zealand. Overlaying the dead portion of the coral matrix are a small group of *Anthomastus* (soft corals), gorgonian *Thouarella* spp. octocorals, hexactinellid sponges, and brisingid sea stars (Image captured by National Institute of Water and Atmospheric Research (*NIWA*), New Zealand, and captured by NIWAs Deep Towed Imaging System (*DTIS*). Credited to NIWA)

serpulid polychaetes or are often entirely devoid of associated fauna. The result is that associated species composition on CWC reefs can strongly vary both horizontally and vertically across the CWC reef ecosystem, but also seasonally.

3.3 Regional (γ) Diversity

The strong evidence for increased numbers of species and sharp zonation patterns in the assemblages of species at CWC reefs underpins the concept of CWC reefs as global biodiversity hotspots (Cathalot et al. 2015). The regional and global species pool (γ diversity) of deep-sea fauna is in large part maintained and enhanced by the distribution of these ecosystems, particularly in the bathyal (200–2,000 m water depth) zone where the majority of CWC reefs occur and where there is a large body of evidence that these ecosystems significantly enhance biodiversity relative to noncoral areas (Henry and Roberts 2007). The huge amount of cryptic diversity revealed by genetics also suggests that endemic morphologically cryptic species could also substantially contribute to γ diversity patterns in the deep sea (Reveillaud et al. 2011), as outlined by Orejas and Jiménez , ▶ Chap. 23, “The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep” in this volume.

Regional CWC reef distribution patterns are critical, because increasing habitat fragmentation by commercial bottom trawling and dredging make it less likely that species and populations can be maintained unless these taxa can overcome the challenges of increasing geographic distance barriers. This makes the role of ocean transport and reef species dispersal capacity supremely important. For example, over the past 25,000 years, maintenance of CWC reefs and their biodiversity in the North Atlantic have directly relied on the supply of coral larvae from adjacent source seas such as the Mediterranean and possibly the Caribbean and South Atlantic Ocean (Henry et al. 2014a and references therein). Both the cold-water reef framework-forming corals themselves and some associated fauna such as sponges exhibit genetic signals that verify a “stepping-stone” phenomena whereby species are connected to adjacent habitat and disperse from there to habitats further away (Henry et al. 2014a). Thus, not only is the enhanced biodiversity and distribution typography of CWC reefs important to the regional seascape but so are the oceanic pathways that connect and maintain species and populations across vast distances (see also ▶ Chap. 38, “Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals” by Costantini and Abbiati in this volume).

It is also becoming well known that CWC reefs are hotspots of global biogeochemical cycling (van Oevelen et al. 2009; Cathalot et al. 2015; Rovelli et al. 2015). For example, CWC reefs of the Træna coral field in Norway had respiration, carbon and oxygen consumption rates, over an order of magnitude higher than in noncoral areas. Thus, another possible way in which CWC reefs may augment γ diversity is by their enhanced capacity to topographically focus or concentrate particles of food to the corals and associated reef fauna over a smaller area. This capacity to baffle sediments and augment currents at the surfaces of all the living coral polyps means that CWCs are potentially capable of drawing significant amounts of organic matter away from adjacent noncoral and soft sediment communities, which may strongly impact not only peripheral α and β diversity in other deep-sea ecosystems but also the overall γ diversity (Cathalot et al. 2015).

4 Knowledge Gaps and Technical Limitations

Core knowledge gaps and limitations of a current synthesis global CWC reef biodiversity include baseline information from areas outside the North Atlantic, habitat use by transient or migratory species, regional biogeography, and cryptic diversity. All are underpinned by a requirement to directly sample habitats and fauna, archive them correctly with accompanying metadata, and by the need to work with standardized protocols, internationally and collaboratively, to ensure the most accurate and robust data are generated.

4.1 Baseline Information in Key Regions

Deep-sea fishing grounds frequently overlap with CWC reefs (see Hinz, ▶ Chap. 37, "Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management" this volume), with some fisheries capable of fishing as deep as 2,000 m water depth. Both fish stocks and CWC reefs benefit from the drawdown of primary production from the sea surface to the seafloor, which interacts with complex topography of CWC reef habitats on the seabed. However, in several cases, both stocks and reefs are in decline as a result of historically unsustainable fisheries effort. The case of orange roughy (*Hoplostethus atlanticus*) is a well-studied example. Globally, the species exhibits a very close association with CWC reefs, and in New Zealand, but paradoxically, there continues to be stock declines in some areas but recovery in others (Doonan et al. 2015). Despite this clear example of habitat destruction and fisheries overexploitation, baseline information on the occurrence, taxonomic identity, species composition, and trophic structure of communities living on most CWC reefs is still lacking. This is particularly true for CWC reefs in the Indian Ocean, Southwest Pacific, and South Atlantic Ocean where studies of CWC reef biodiversity only began in 2013 in contrast to areas like the North Atlantic and Mediterranean (Fig. 4). The lack of information makes it difficult to ascertain what the natural or desired state of a CWC reef should be in order to develop appropriate management and conservation measures. Some CWC reefs are afforded a special status at the highest international level through the Food and Agriculture Organization of the United Nations (FAO) definition as a vulnerable marine ecosystem (VME) because of this fisheries overlap and the coral habitat's limited capacity to recover: yet there is a limited scientific evidence base in each of these regions as to

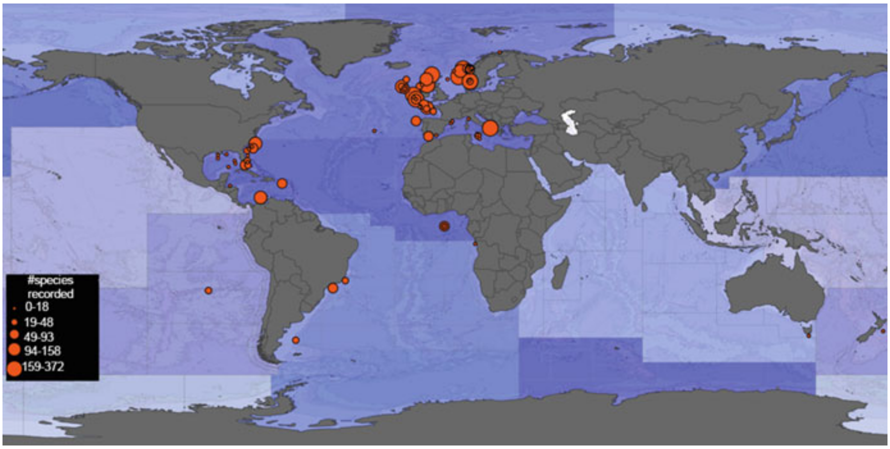

Fig. 4 Review of the literature on CWC reef biodiversity showing numbers of associated animal species found (as of early 2013). FAO major fisheries regions are shown by different shades of *blue*, with FAO subareas delineated within each major region. Note the lack of studies (as of 2013) in FAO major fisheries regions including the western and eastern Indian Ocean, southwest Pacific Ocean, and the southwestern and southeastern Atlantic Ocean, despite the known occurrences of the six major reef-building azooxanthellate species (Fig. 1)

what species are characteristic of these reefs and the potential for these reefs to act as hotspots of biodiversity and biogeochemical cycling.

4.2 Habitat Use by Migratory Animals

The lack of studies on transient or wide-ranging migratory animals using CWC reef habitat means that biodiversity studies in these ecosystems may have underestimated biodiversity and importance of these habitats to these animals, and possibly this has led to an oversimplification of CWC reef food webs. There have been no studies as to whether marine cetaceans interact with CWC reefs, and most studies of the reef fish fauna provide only a snapshot of the communities at any one time. Sustained sampling campaigns are needed, but these must be conducted so as to minimize environmental damage.

Complementary approaches could include investigation of longer-term migratory animal habitat use through the use of nonlethal techniques such as multitissue stable isotopes obtained from blood or tissues to elucidate trophic structure and partitioning and whether the animal derives most of its energetic resources from CWC reefs or elsewhere. Telemetry is also a rapidly evolving tool involving tagging and tracking migrating animal populations over short and long time periods, with transmitters now capable of archiving significant amounts of environmental metadata to link the time spent in a particular habitat as well as the drivers keeping them there or triggering them to move away. Evidence for fish aggregations, spawning sites and nurseries in CWC reefs (D'Onghia et al. 2012), year after year at similar sites (Henry et al. 2013b), suggests that telemetry has the potential to help elucidate habitat specificity and residency in migratory and transient animals and thus contribute to significantly improving our understanding of how CWC reefs support ocean biodiversity.

4.3 Regional Biogeography

A greater understanding of how species are distributed in the deep sea allows stakeholders to prioritize management decisions such as selecting representative marine protected areas (MPAs) and ensuring that an MPA network allow for the connectivity of marine genetic resources (Rice et al. 2011; see also ▶ Chap. 34, "Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest" by Rice and Smith; ▶ Chap. 38, "Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals" by Costantini and Abbiati; ▶ Chap. 35, "The Impact of Anthropogenic Activity on Cold-Water Corals" by Grehan et al. in this volume). The lack of standardized, systematic surveys in deep-sea ecosystems across the globe makes it difficult to synthesize data at spatial scales relevant to management. In the case of CWC reefs, there is sometimes very detailed knowledge of particular local systems. However, scaling up observations to other areas into a broader regional or global synthesis must be carefully undertaken, especially as sampling effort, gear, taxonomic expertise, and resolution may vary widely across studies. Some intraregional biogeographic analyses from CWC reefs have been made for associated sponge (Van Soest and de Voogd 2013) and hydroid (Henry et al. 2008) fauna across scales of 100s to 1,000s of kms, which refuted (in the case of sponges) and supported (in the case of hydroids) existing deep-sea biogeographic classifications based simply on direction of prevailing ocean currents.

Another confounding factor in tackling the challenge of species biogeography in the deep sea is that the ocean circulation and its properties constantly change on annual to millennial time scales. Oceans are also currently undergoing unprecedented rates of changes in temperature and carbonate chemistry regimes, with the expansion of oxygen minimum zones around the globe also expected to profoundly affect deep-sea processes and the distribution of life forms, e.g., by compressing available habitat for pelagic fish (Stramma et al. 2012). Thus, biogeographic classifications using historic collections obtained decades to over a century ago will very likely be inaccurate. Deep-sea species biogeographic boundaries are dynamic and very likely have transitional or unclear borders (Rice et al. 2011); thus, any attempt at rectifying the regional or global biogeography of CWC reefs must consider the oceanic regime in which the basic units of the biogeographic classification (species, environmental parameters) were collected. Essentially, any robust marine biogeographic classification should strive for four-dimensionality (latitude, longitude, depth, and time) to capture this dynamic nature.

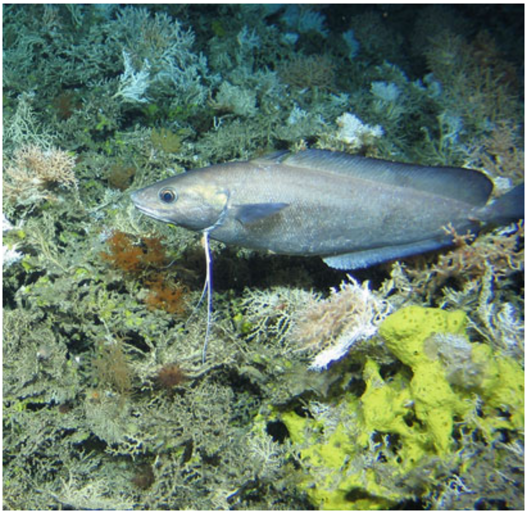

Fig. 5 Cryptic diversity on CWC reefs is hidden all around. The bright *yellow* sponge in the foreground, *Hexadella* cf *dendritifera* (aprox. 684 m) can densely colonize the mixed live/dead coral zone in the northeast Atlantic but molecular analyses revealed hidden diversity in morphologically similar sponges from the Ionian Sea in the Mediterranean to the Greenland Sea (Reveillaud et al. 2010) (Image credited to Heriot-Watt University and NERC)

4.4 Cryptic Diversity

Morphologically similar species may also exhibit varying levels of genetic differentiation, which has led to the vast underestimation of species diversity on CWC reefs and probably β and γ diversity as well. Cryptic species are becoming especially well-documented in the sponges associated with CWC reefs (Reveillaud et al. 2010, 2011), for example, in the genera *Hexadella* and *Plocamionida* (Fig. 5) which suggests there is far greater hidden species diversity than previously thought in these ecosystems.

5 Frontiers in Technology

Technological developments in deep-sea exploration continue to advance, driven mainly by the military applications and the need for increased understanding and exploitation potential of deep-sea resources. Deep-sea investments by traditional sectors including the petroleum industry and subsea telecommunications continue to grow particularly in deepwater oil and gas extraction but also from rapidly emerging industries such as blue biotechnology and deep-sea mineral mining businesses. Other sectors such as human health and agriculture have also enabled translational genomic technologies to open up new frontiers in the science of CWC reefs across the globe.

At the frontier of these technology developments are multisensory lander platforms, observatories, robotics, and genomics, all of which have been in service on land for many years, but which now offer extremely powerful tools with which a deeper understanding of CWC reef and deep-sea biodiversity can be obtained.

5.1 Landers and Observatories

Seafloor lander platforms offer the potential to obtain longer-term (several hours to years) in situ observations of the CWC reef environment and associated biodiversity. Landers became more routinely deployed in CWC reefs since the early twenty-first century (Roberts et al. 2005) and were typically equipped with standard instrumentation such as stills or video cameras, sediment traps, and acoustic Doppler current profilers (ADCPs) allowing for variations in current strength, temperature, and salinity to be measured. Frontiers in lander technology include significant enhancements in sensor modalities including carbonate chemistry and eddy covariance measures that use delicate probes and sensors to obtain very high resolution measurements of oxygen to understand how CWC reef biodiversity is linked to ecosystem functioning (Rovelli et al. 2015).

Cabled seafloor observatories in CWC reefs offer yet another tool to obtain novel observational data on environmental dynamics and species habitat use in relation to these properties. Since 2013, the petroleum company Statoil has maintained the LoVe Ocean Observatory at a CWC reef in approximately 255 m water depth off the Norwegian coast. LoVe offers free, near real-time camera stills, timelapse video, hydrophone, and fisheries acoustic data. Also included are packages for temperature, salinity, pressure, conductivity, turbidity, chlorophyll, organic, and suspended matter. Observatories such as these could help greatly advance the understanding of temporal dynamics in CWC reef biodiversity, especially with respect to camera-shy fish that may avoid large remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUVs) navigating the reef, but also the transient or migratory species that are not captured by snapshots during a cruise.

5.2 Robotics and Engineering

Surveys of CWC reef biodiversity are often conducted by means of specially engineered grabs, cores, stills, and video cameras mounted on landers, dropped systems, or as part of an ROV package or cabled seafloor crawler. It is vital that these surveys obtain actual samples of reef fauna to validate species identification and offer the potential for genetic studies to further refine species' boundaries. Sometimes this is not possible, and all that exists are images or videos of megafauna. Improvements and bespoke design of all types of sampling gear, such as videograbs specialized for collecting and retaining coral framework and smaller mobile and sessile epifauna, continue to be made. Off the shelf and specialized ROVs are now smaller, more manoeuvrable, have longer battery-lives, and in many cases are now capable of remote manipulation by means of dextrous arms or claws. Many vehicles also provide ample storage and additional sensor packages to obtain accompanying environmental metadata in deep-sea habitats and can return excellent quality images from the seafloor, a significant advancement beyond the very first low-resolution monochrome images. Internet-operated and cabled deep-sea crawlers are also emerging technologies for this frontier (Purser et al. 2013a).

Unlike ROVs that must remain tethered and powered to a surface vessel, AUVs are yet another significant and possibly more cost-effective advancement in the technology used to study CWC reefs. Tetherless platforms are especially good candidates to consider when implementing research and monitoring programmes in complex fragile environments such as coral reefs. AUVs have already proved vital to locating and mapping CWC mounds in the North Atlantic off Florida and in the northern Rockall Trough (Wynn et al. 2014). Some AUVs are hover-capable and ensure very precise station keeping. Autonomous manipulation is still very much an engineering frontier, but these tasks are also proving possible in trials at sea, which would open the possibility of autonomous sampling of target organisms. Some AUVs are also capable of tracking chemical plumes such as those simulated in carbon capture carbon storage facilities leaks and pollution outfalls. Other AUVs can even track migratory species like sharks and other fish in deep waters better than shipboard methods (Eiler et al. 2013), a capacity that should be explored in more detail for CWC reef habitats where there is little information on habitat use by these species.

The vast volumes of image, video, and acoustic data collected during modern CWC reef surveys is a challenge to studying biodiversity in these ecosystems, with much research effort, expertise, and cost attributed to annotating, mapping, and interpreting data. Computer-aided technology such as machine-learning algorithms is now being implemented on CWC reef datasets. These automated detection methods can potentially offer far more cost-effective, and even more accurate, solutions than those provided by experts who undertake classic point annotations (Purser et al. 2009). The ultimate goal is to be able to undertake accurate, reliable, and completely unsupervised segmentation and classification in real-time on board an autonomous system during each CWC reef mission.

5.3 Genomics

Recent advances in next-generation sequencing techniques such as restriction site-associated DNA sequencing (RADSeq) of single nucleotide polymorphisms (SNPs) now make rapid economic screening of marine genetic resources in the deep sea possible, even for organisms without reference genomes (Herrera Monroy 2015). These advances greatly facilitate obtaining answers to knowledge gaps in population genetics, species boundaries, and evolutionary genetics, especially as it pertains to adaptive potential under different scenarios of climate change (Herrera Monroy 2015). The potential to screen and monitor deep-sea biodiversity with samples of environmental deoxyribonucleic acids (eDNA) is also being validated in deep-sea systems such as canyons (Guardiola et al. 2015), an approach that could also be applied in the context of CWC reef ecosystems as part of a management toolkit.

6 Conclusion and Future Directions

Cold-water coral reefs are global biodiversity and biogeochemical cycling hotspots and play host to thousands of animal species throughout the ocean food web. CWC reefs not only enhance species diversity and harbor distinct assemblages across the reef structure but these ecosystems also enhance regional and global diversity.

Large gaps in the knowledge of global CWC reef biodiversity still exist. The overwhelming majority of biodiversity studies come from the North Atlantic, yet major azooxanthellate reef-building scleractinians are globally distributed. Particular knowledge gaps are in the Southwest Pacific, South Atlantic, and Indian Ocean, and like the North Atlantic and Mediterranean, very likely overlap socioeconomically important fishing grounds. Generally, there are still too few studies on habitat use by migratory species like sharks; certainly, the more undersea images from CWC reefs that are examined in close detail, the more that gains to be discovered in these habitats such as possible shark spawning grounds (Fig. 6). It is also not known to what extent deep-diving marine mammals may use CWC reefs. The lack of standardized, systematic surveys of the biodiversity on CWC reefs prevents regional and global syntheses in most cases; where they have been possible, such analyses provide new insight into biogeographic boundaries and their possible environmental drivers. Molecular genetics are revealing substantial levels of cryptic or hidden diversity among the sponges associated with CWC reefs and suggest that the global biodiversity of CWC reefs has been vastly underestimated.

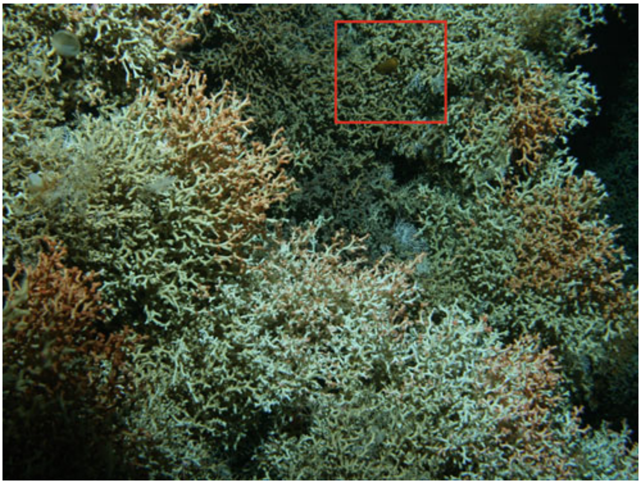

Fig. 6 A shark egg (bounded by *red box*) deposited amongst the dense thickets of the live reef-forming branching stony coral *Solenosmilia variabilis* at a depth of 996 m on the seamount Gothic in the Graveyard Knoll area, Chatham Rise, southeast New Zealand. Some dead coral matrix is also visible along with delicate lacy stylasterid hydrocorals and small hexactinellid sponges (Image provided by the National Institute of Water and Atmospheric Research (*NIWA*), New Zealand, and captured by NIWAs Deep Towed Imaging System (*DTIS*). Credited to NIWA)

The future of CWC reef biodiversity science will still rely on the fundamentals of direct sampling of habitats and fauna, which are then properly archived along with any accompanying metadata. This means that institutional links with private industries such as fisheries, oil and gas, deep-sea mining, and the public sector including governments and museums and sustained funding streams for archival work must be more firmly established. The science will also still rely on the need for standardized protocols developed internationally and collaboratively across disciplines.

Frontier technology has a huge role to play in advancing CWC reef biodiversity science across the globe. Landers and observatories provide much-needed long-term environmental time series with which biodiversity data can be matched to understand environmental drivers of species diversity and community change. These platforms also provide new insights into camera shy or transient visitors to the reefs. ROVs, AUVs, and further automation offer CWC reef biodiversity science opportunities to significantly advance how these ecosystems are studied at every step, from conducting mission across the reef, to in situ sample manipulation, to species annotations. Next-generation genomics provide the necessary genetic validation of species boundaries and will allow for a far deeper understanding of the evolutionary adaptations of species and lineages in a deep undersea world heralding great changes in the ocean.

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