

Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems

J. Murray Roberts,¹ Andrew J. Wheeler,² André Freiwald³

Coral reefs are generally associated with shallow tropical seas; however, recent deep-ocean exploration using advanced acoustics and submersibles has revealed unexpectedly widespread and diverse coral ecosystems in deep waters on continental shelves, slopes, seamounts, and ridge systems around the world. Advances reviewed here include the use of corals as paleoclimatic archives and their biogeological functioning, biodiversity, and biogeography. Threats to these fragile, long-lived, and rich ecosystems are mounting: The impacts of deep-water trawling are already widespread, and effects of ocean acidification are potentially devastating.

Cold-water corals have been known since the 18th century. Only recently, as fishery and oil exploration activities in deeper waters have increased, have developments in acoustic survey techniques and access to submersibles revealed the scale and abundance of cold-water coral ecosystems (1, 2). Corals occur individually, as isolated colonies, in small patch reefs several meters across, or they form large reefs and giant carbonate mounds up to 300 m high and several kilometers in diameter over many thousands to millions of years. Because of their age and growth rates, reefs contain high-resolution records of long-term climate change and may also be important speciation centers in the deep sea. Recent research suggests a coupling between the reef fauna and surface productivity, with reef development controlled by the interplay of local hydrography and sedimentary dynamics.

Corals, Reefs, and Carbonate Mounds

Cold-water corals are cnidarians encompassing stony corals (Scleractinia), soft corals (Octocorallia, including “precious” corals, gorgonian sea fans, and bamboo corals), black corals (Antipatharia), and hydrocorals (Stylasteridae) (Fig. 1). They are azooxanthellate (i.e., lacking symbiotic dinoflagellates) and often form colonies supported by a common skeleton, providing structural habitat for other species. Here we focus on scleractinian reef framework-forming species. Gorgonian and antipatharian corals, although not reef-forming, can develop dense assemblages that form important structural habitats (Fig. 1). These are mostly

value as paleoclimatic archives is discussed below.

Species, habitats, and ecosystems discussed here are distinct from those of tropical coral reefs and are specifically associated with colder conditions, often in deep offshore waters (3). Reefs and mounds tend to cluster in “provinces,” where specific hydrodynamic and food supply conditions favor coral growth. Some

provinces are characterized by small mound features; e.g., the Darwin Mounds in the northern Rockall Trough (4, 5), or giant carbonate mounds where reefs have become repeatedly established since the Late Pliocene/Pleistocene; e.g., in the Porcupine Seabight, NE Atlantic (6, 7).

Reef Distribution, Genesis, and Development

Cold-water corals are largely restricted to oceanic waters and temperatures between 4° and 12°C. These conditions are generally found in relatively shallow waters (~50 to 1000 m) at high latitudes, and at great depths (up to 4000 m) beneath warm water masses at low latitudes. Approximately 800 species of reef-building scleractinians are described in shallow waters, yet fewer than 10 are known to make substantial deep-water reef frameworks (1, 8). Of these, we have an incomplete view of their global distribution (Fig. 2), which remains skewed by the geographically varied levels of research activity and the bias of deep-water mapping initiatives to the developed world. Despite this, some intriguing patterns in their global biogeography are becoming evident. Cold-water scleractinian species diversity is highest around the Philippines, with global distribution influ-

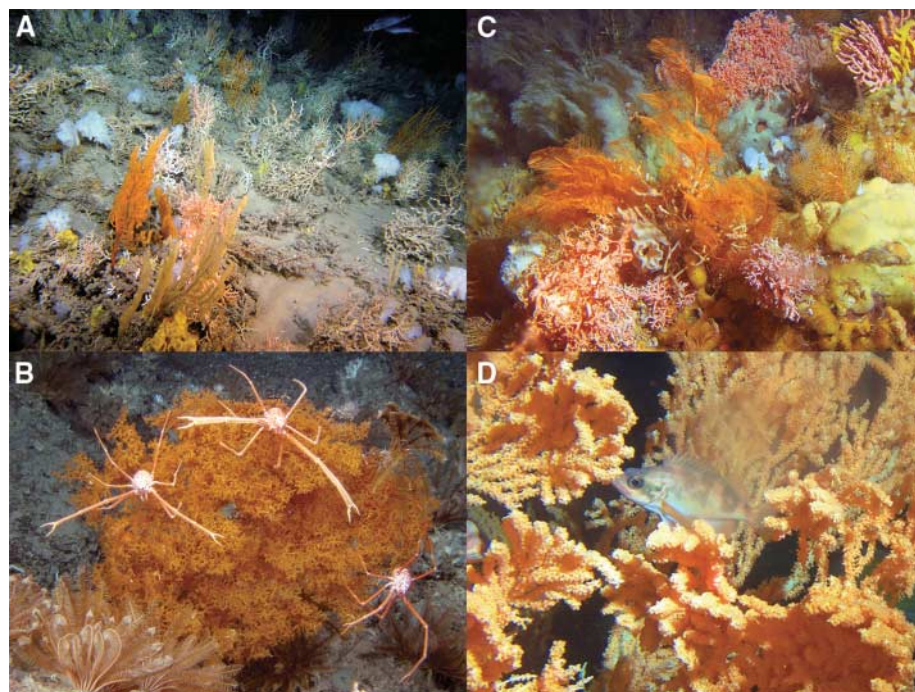


Fig. 1. Cold-water coral reef fauna. (A) Sloping flank of the Galway carbonate mound colonized by scleractinian and gorgonian corals and glass sponges. (B) Currently undescribed antipatharian coral (*Leiopathes* sp., pers. comm. D. Opresko) and associated anomuran crustaceans from the Twin Mounds, Porcupine Bank (NE Atlantic). [Images courtesy Alfred-Wegener-Institut für Polar und Meeresforschung and Institut Français de Recherche pour l'Exploitation de la Mer] (C) Diverse coral and sponge fauna recently discovered off the Aleutian Islands. [Image courtesy of A. Lindner, National Oceanic and Atmospheric Administration (NOAA) Fisheries] (D) Sharpchin rockfish (*Sebastes* sp.) among gorgonian corals (*Primnoa* sp.) in the Gulf of Alaska (N Pacific). [Image courtesy of V. O'Connell, Alaska Department of Fish and Game]

¹Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll, PA37 1QA, UK. ²Department of Geology and Environmental Research Institute, Donovan's Road, University College Cork, Cork, Ireland. ³Institute of Paleontology, Erlangen University, Loewenichstrasse 28, D-91054, Erlangen, Germany.

enced by seawater carbonate chemistry (9). Recent work shows a striking relationship between the number of cold-water scleractinian occurrences and the depth of the aragonite saturation horizon (ASH). This may help explain the abundance of coral records in the NE Atlantic, where the ASH is >2000 m deep, compared with the paucity of records from the N Pacific, where the ASH is as shallow as 50 to 600 m and the coral fauna is dominated by octocorals and stylasterids (9, 10).

Reefs develop after an initial settlement of a coral larva to a hard substratum. As a coral grows, polyps in older portions die, and the skeleton becomes increasingly vulnerable to bioeroders (notably, clionid sponges) and mechanical breakage. Bioeroded skeletons may break, fall to the seabed, and extend the perimeter of the reef patch. These processes are fundamental in creating the reef framework that, over time, baffles and traps mobile sediment. Provided that coral growth keeps pace with sediment infill, localized mound formation is initiated (11, 12). The development of deep-water reef mounds and their colonization can be thought of in a cyclical sense, with the associated community predicted to vary with the stage of reef development and available microhabitats (Fig. 3).

Lophelia pertusa reefs on the Norwegian shelf and carbonate mounds in the Porcupine Seabight were thought to be related to light hydrocarbon seepage, a concept later developed into a hydraulic theory of cold-water coral reef development (13). However, isotopic compositions of coral skeleton and tissue are not compatible with a seepage-based food chain (14), and although some reefs are reported close to seeps and pockmarks, many, if not most, are not. In May 2005, the International Ocean Drilling Program (IODP) Expedition 307 drilled to the base of the Challenger Mound in the Porcupine Seabight and found no gas accumulation beneath or within the mound and no evidence that mound growth was initiated by hydrocarbon seepage (7). Conversely, mound growth appears to be initiated at several sites over a wide area upon an unconformity followed by a rapid period of mound growth and coalescence. We believe this may indicate that clusters of small mounds may, over time and under favorable environmental conditions, form giant carbonate mounds.

Trophic Dynamics

Unlike the predictions of the hydraulic theory, recent research shows that cold-water corals are

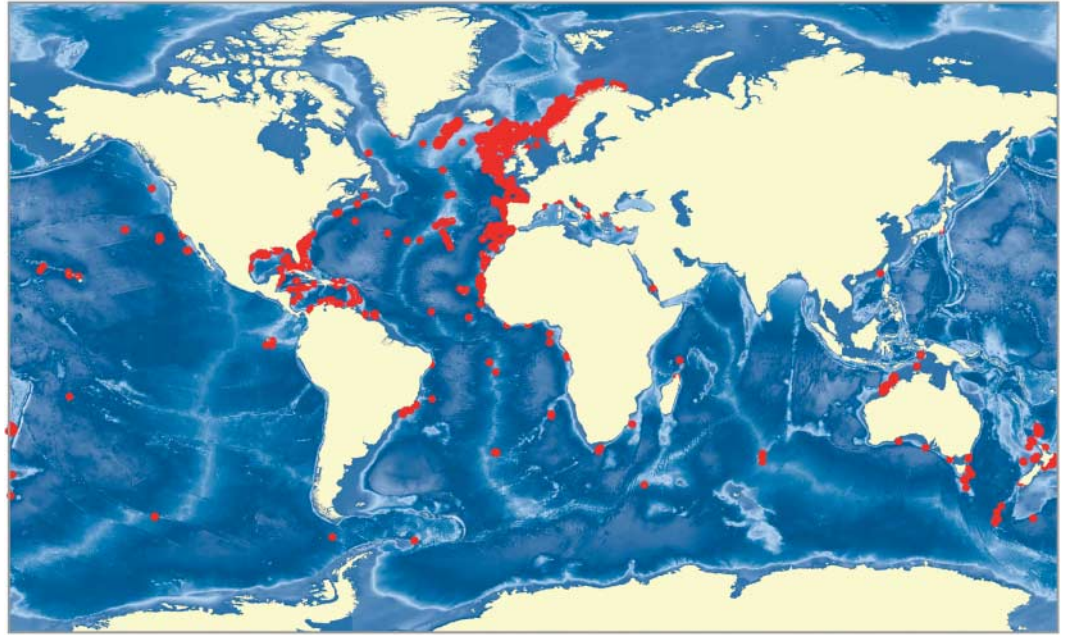


Fig. 2. Current global distribution of reef framework-forming cold-water corals [modified from (1)].

fueled by primary productivity in surface waters and subsequent food transport to the sea floor (14). Corals are frequently reported from sites with locally accelerated currents, or from areas of the continental slope where internal tidal waves enhance seabed food supply. Around topographic highs, such as the Porcupine Bank in the NE Atlantic, currents trap nutrient-rich waters above the bank that, under certain conditions of bottom slope and density stratification, may drain slowly off-slope through the benthic boundary layer (Ekman drainage) and supply food to the coral reefs associated with large carbonate mounds on its slopes (15). Recent studies in the Darwin Mounds found fresh labile material, including lipids and polyunsaturated fatty acids, present at depths of almost 1 km (16). Coral lipid and nitrogen isotope compositional analysis suggests that *L. pertusa* and *Madrepora oculata* rely predominantly on a zooplankton diet; but compared with *M. oculata*, *L. pertusa* is enriched in monounsaturated fatty acids and $\delta^{15}\text{N}$, has far larger polyps, and has been seen capturing live zooplankton in the field. It is therefore possible that these two species adopt different feeding strategies, although species-specific metabolic differences cannot be ruled out (17). Recent work on shallow-water scleractinians reinforces the view that corals are cosmopolitan consumers able to feed from suspended sediments, dissolved organic matter, bacteria, protozoans, and both zoo- and phytoplankton (18). Detrital and resuspended materials are likely to be important food sources for corals in deep waters. Sediment-trap studies show that phytodetritus, fecal pellets, and zooplankton were the most substantial sources of particulate carbon available to cold-water coral communities on Galicia Bank in

the NE Atlantic (14). Although currently unquantified, diurnally migrating zooplankton and over-wintering populations of calanoid copepods are likely to be ecologically important prey items.

Reproductive Ecology and Population Genetics

Little is known about the reproduction of cold-water corals, despite its fundamental importance. Most shallow-water scleractinians are hermaphrodites, but the majority of cold-water corals studied to date are gonochoristic (have separate sexes). Seasonally enhanced food flux associated with spring phytoplankton blooms greatly influences benthic carbon flux and reproductive periodicity in deep-sea fauna. In the NE Atlantic, it seems that gamete production in *L. pertusa* follows phytodetrital food fall, and this species is likely to spawn before the following spring (19).

The application of molecular tools to cold-water coral populations is a powerful approach to elucidate taxonomic and systematic relationships. For example, ribosomal RNA (rRNA) sequencing suggests that *M. oculata* may have been historically misclassified (20). The degree of reef connectivity can also be examined by using a molecular approach. Microsatellite and ribosomal internal transcribed spacer (ITS) sequence analyses indicate that *L. pertusa* is not a panmictic population in the NE Atlantic but seems to form discrete fjord and shelf populations (21). In the Darwin Mounds, microsatellite analysis shows that the coral population is clonal (21), and a histological study found no reproductive corals (22). In the Pacific Ocean, microsatellite studies suggest that the precious gorgonian coral *Corallium*

lauuense is suffering inbreeding depression on Hawaiian seamounts, perhaps because of fishing pressure for its skeleton, which is used in jewelry making (23). Such information is vital to develop conservation policies, and we anticipate major advances in this area in the coming years as more genetic markers are developed and applied.

Biodiversity and Endemism

Cold-water corals are arguably the most three-dimensionally complex habitats in the deep ocean, providing niches for many species. For example, we know that over 1300 species have been found living on *L. pertusa* reefs in the NE Atlantic (24). Their biodiversity may be comparable to that found on tropical coral reefs, but few quantitative studies allowing regional comparisons have been made. We understand little of the functional relationships between species on cold-water coral reefs, and the reefs' importance as a fish habitat is unclear (8).

We also understand little of the connectivity between reef provinces. Seamounts trap ocean currents producing localized circulation patterns. Under these conditions, larvae could be retained, which would limit species' dispersal, promote local adaptation, and potentially enhance rates of speciation (25). Although very few of the estimated 30,000 to 50,000 seamounts have been studied, species endemism appears to be high. For example, up to 34% of species on SW Pacific seamounts were newly discovered and potentially endemic. Because there were few common species between seamounts in this region, it is possible that, especially along ridge systems, seamounts may be analogous to island groups (26). Cold-water coral reefs are frequently reported from seamounts; therefore, given their species diversity, propensity to localized circulation patterns, and longevity, cold-water coral reefs may be major speciation centers.

Longevity and Paleoclimatic Archives

Cold-water coral reef and mound development in the NE Atlantic reflect environmental change over geological time scales corresponding to recurrent glacial cycles. In northern Europe, Scandinavian reefs date from the Holocene after the retreat of the Pleistocene ice sheet ~10,000 to 14,000 years ago. Stratigraphic studies from the giant carbonate mounds off Ireland show pronounced depositional cycles of coral-rich and hemipelagic sedimentation associated with glacial-interglacial periods extending back to at least the early Pleistocene, albeit with substantial hiatuses (7, 12). In the Mediterranean Sea, off NW Africa, and on the mid-Atlantic ridge beyond the southern limit of the ice sheets, U/Th dating suggests continuous cold-water coral growth over the last 50,000 years (27). Given that reef framework-forming corals such as *L. pertusa* cannot survive in water masses <4°C but can rapidly colonize new anthropogenic substrata (28), it seems like-

ly that high-latitude reefs have repeatedly diminished during glacial periods and flourished during interglacial periods. This would limit their potential role as speciation centers. Conversely, we suggest that coral ecosystems at lower latitudes, especially those on seamounts where biodiversity and endemism are known to be high, are likely to be important speciation centers and glacial refugia in the deep sea.

Given their longevity over geological time scales, cosmopolitan distributions, and banded skeletal structure, cold-water corals are important paleo-environmental archives. There are two broad categories of studies: (i) those that estimate past seawater temperatures from skeletal chemistry and (ii) those that follow the ventilation history of the ocean by dating skeletal material. Both are fundamental in reconstructing climate history.

Stable oxygen isotopes from biogenic carbonates have been used for many years to estimate paleo-seawater temperatures and salinities. However, scleractinian coral skeletons do not form in isotopic equilibrium with seawater, and in

azooxanthellate corals, stable isotopes of oxygen and carbon are strongly correlated. These kinetic effects may relate to the rate of coral calcification that is probably driven by seasonal factors: notably, annual phytodetrital deposition (29). Despite this, stable isotopes from cold-water corals have been used to derive seawater temperatures (30). Interpreting chronologies from scleractinian framework-forming species like *L. pertusa* is complicated by cryptic banding patterns and complex skeletal morphologies, even though they are widespread and well-preserved in the fossil record. Recent work on *Enallopsammia rostrata* shows that even though the banding pattern is not annual, it may be possible to interpret annual chronology using ²¹⁰Pb as a time proxy (31). There is now good evidence that the tree-like stems of cold-water octocorals are annually banded (32), unlike *E. rostrata*, and Mg/Ca ratio analysis of gorgonian and bamboo corals has yielded convincing paleo-temperatures (33, 34).

Shifts in deep-ocean circulation patterns profoundly affect global climate, and there is now

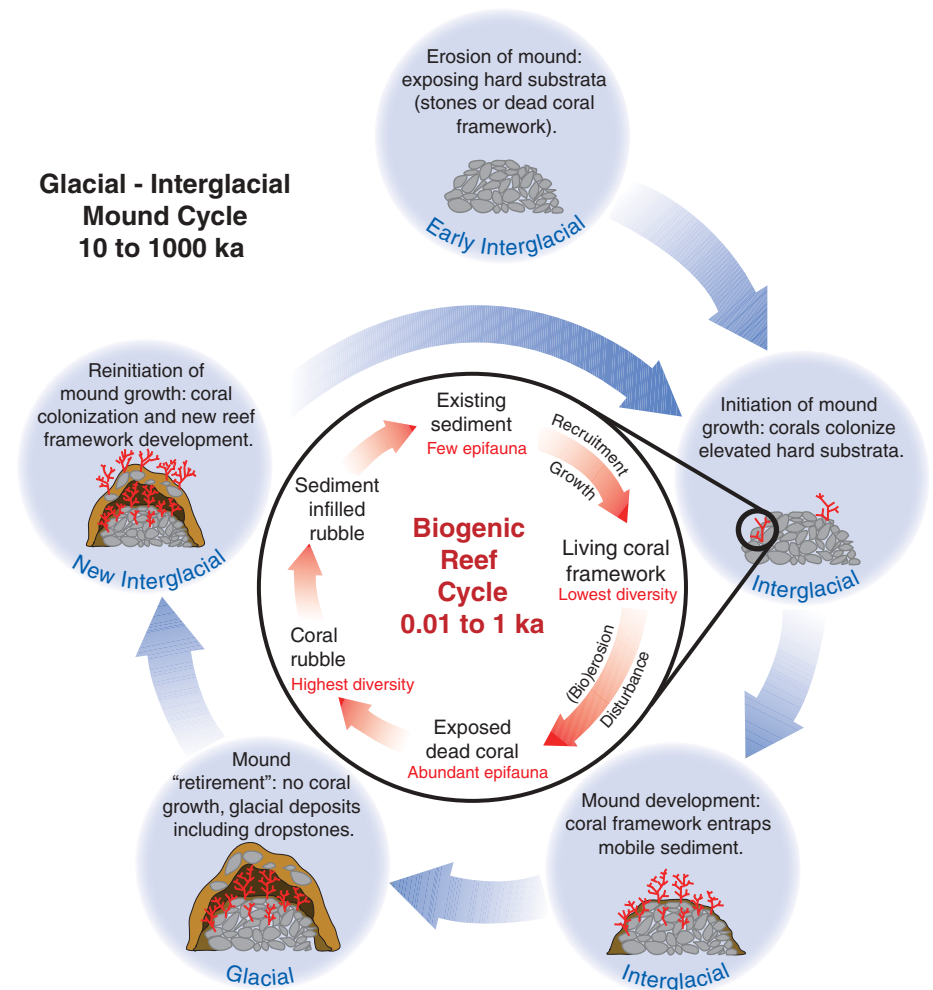


Fig. 3. Schematic illustration showing the following: (**Outer circle**) Cyclic stages of carbonate mound growth from initiation, development, retirement, and recolonization. (**Inner circle**) Smaller scale cycle of reef microhabitats, succession, and faunal diversity.

evidence that cold-water corals have recorded these oceanic shifts in their skeletons. Because U/Th dating yields coral age and ^{14}C dating provides coral age plus the age of the inorganic carbon in seawater, complementary U/Th and ^{14}C studies infer the age of the seawater in which the coral grew (35). Adkins *et al.* (36) suggest that the solitary coral *Desmophyllum cristagalli* experienced shoaling of “young,” low-nutrient North Atlantic deep water and replacement with “old,” high-nutrient southern source water. Shoaling of more than 200 m occurred very rapidly, i.e., during the coral’s 160-year lifetime, and coincided with the transition to the Bølling-Allerød warming period. This approach has now been used to study ventilation histories in the Southern Ocean (37) and North Atlantic (38).

Threats

Although we are only now starting to realize the ubiquity of cold-water coral reefs, their biodiversity, and value as paleoclimatic resources, human activities threaten these ecosystems in three ways: (i) bottom trawling causes damage, (ii) hydrocarbon drilling and seabed mining have potential impacts, and (iii) ocean acidification has potentially severe effects on calcifying reef fauna.

There is global evidence that these habitats have been damaged by trawling for deep-water fish, causing severe physical damage from which recovery to former reef status will take several hundreds or thousands of years, if at all (Fig. 4) (1, 39–41). Several nations, including Canada, Norway, UK, and USA, have responded by closing cold-water coral habitats to bottom fishing. Beyond territorial waters on the High Seas, no individual nation has jurisdiction, and any conservation measures would need to be developed using the United Nations Convention on the Law of the Sea (1).

Compared with widespread evidence for physical damage to reef structures from bottom trawling, there is little evidence that hydrocarbon exploitation substantially threatens cold-water

coral ecosystems. *L. pertusa* colonizes North Sea oil platforms and seems to have formed a self-seeding population, despite proximity to drilling discharges (42). Greatest concern is over the potential for drill cuttings to smother reef fauna (43), but such effects would be highly localized when compared with the extent of seabed affected by bottom trawling. To date, there has been little interest in mining the rich mineral deposits found in some seamounts and along oceanic ridge systems. However, mining activities risk causing local extinctions on seamounts supporting endemic species.

Perhaps the most insidious threat to cold-water coral reef ecosystems is from ocean acidification. There is general consensus that atmospheric carbon dioxide levels are rising sharply, and modeled scenarios suggest that this could cause the greatest increase in ocean acidification over the last 300 million years (44). Current research predicts that tropical coral calcification would be reduced by up to 54% if atmospheric carbon dioxide doubled (45). There have been no studies to examine these effects on cold-water corals, but given the lowered carbonate saturation state at higher latitudes and deeper waters, these species may be even more vulnerable. In addition to the effect acidification could have on coral calcification, modeling studies predict that the depth at which aragonite dissolves could shallow by several hundred meters, thereby raising the prospect that areas once suitable for cold-water coral growth will become inhospitable (10, 45, 46).

Conclusions

This Review highlights recent major advances in our understanding of cold-water coral ecosystems after intensified research efforts across the biological and geological sciences. Of particular importance are studies into paleoclimatic archives, biodiversity, and habitat destruction. Emerging concepts are the importance of cold-water coral reefs as speciation centers and deep-water glacial refugia, major threats posed by the impacts of ocean acidification, and evidence confirming hydrodynamic biogeological carbonate mound growth processes. We expect to see continued advances in many areas, particularly reproductive and genetic studies, biogeography, spe-

cies interaction, and ecological studies where time series of data are required. Sea floor observatories are anticipated to play an important future role (47).

Despite the inherent difficulties of studying these habitats, there is an urgent need for sound information on which to base long-term management plans. Bottom trawling, often on the High Seas, has damaged cold-water coral ecosystems, and we do not understand the long-term implications of ocean acidification. The vast majority of cold-water coral reef studies so far are from the developed world; therefore, a need exists to transfer expertise in deep-water surveys to the developing world and to begin unified ocean basin-scale comparisons if we are to appreciate the global connectivity and importance of these reefs of the deep.

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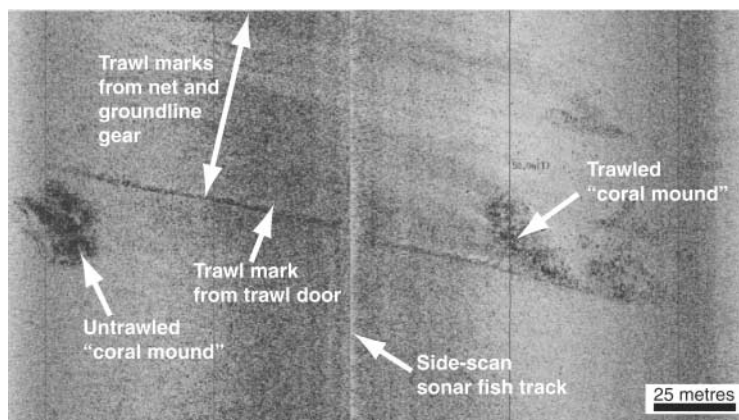


Fig. 4. Side-scan sonograph showing trawl damage to the Darwin Mounds at almost 1-km water depth in the Rockall Trough (NE Atlantic). Reduced backscatter (lighter tones) from the trawl-damaged mound strongly suggests decreased coral abundance [modified from (5)].

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Supporting Online Material

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