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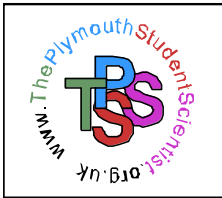
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Deep-Sea Coral Reefs: Distribution, Ecology & Anthropogenic Impacts

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Abstract

The introduction of Remotely Operated Vehicles (ROVs) and manned submersibles has meant scientists can finally begin study deep-water scleractinian coral reefs, making valuable first-hand observations of the reefs themselves and their associated fauna. Known influences of deep-water coral reef distribution include the topography of the seabed, presence of currents, high nutrient levels and low sedimentation levels. Chemical tolerances (such as salinity, temperature range and calcium carbonate availability) are mostly known for only *Lophelia pertusa* corals. Debates exist within literature over the possible influence of hydrocarbon seeps from the seabed on coral reef growth and distribution.

Studies show the importance of deep-water coral reefs as habitat for fish and invertebrates. Some faunal habitat associations have been looked at, yet not studied in detail. The majority of this research has looked for fish association with the deep-water coral reefs. Proposed reasons for these associations include the reef habitat being a structural refuge from predation, a suitable feeding habitat and a protective nursery for juvenile fish. There are relatively few studies undertaken into the presence of other faunal groups on deep-water coral reefs, though there is some qualitative data obtained from analyses of fish stomachs.

Benthic trawling for commercial fish spp has, over the years, destroyed large portions of deep-water coral reefs. The future predicted rise in atmospheric CO₂ may also impact this habitat detrimentally by altering the chemistry of the seawater. For such slow-growing, fragile organisms as corals, these habitat losses may never be regained.

Introduction

The existence of deep-sea coral reefs has been known for over 100 years (Hatcher & Scheibling, 2001). However, unlike their shallow water counterparts, very little is known of deep-sea coral reefs. This is because it is only in recent years that technology has enabled scientists to gain first-hand knowledge into the deep-sea's unseen, aphotic expanse. Indeed, it is often said that 'we know more about the surface of the moon than we do about the sea floor' (SAMS, 2005).

The past decade has brought the valuable introduction and use of new technologies with which to better study the ecology of deep ocean floor habitats. The use of Remotely Operated Vehicles (ROVs) and manned submersibles has meant scientists can finally observe deep-water, benthic organisms in their natural environment; permitting studies into their true habitat associations, behaviours and hypotheses regarding ecosystem functions. Prior to the availability and use of such technologies, much of our understanding of these habitats was based on fisherman's reports of trawling the seabed and what they had found. Any inferences (eg about organism habitat associations) derived from trawl data may be misleading. For example, though habitat associations could be assumed due to the catch of a certain organism in the same trawl as a deep-water coral fragment, the trawl could be taken over different types of benthic habitat; thus the organism in question may have been located in a non-reef habitat (eg seabed) far away from the coral. Furthermore, many habitat fragments caught within a trawl net are unidentifiable. Therefore, many trawl-derived organism data is merely qualitative and cannot be treated as a valid quantitative survey of a benthic habitat (Ross & Quattrini, 2007).

In contrast to this unreliability of data gleaned from benthic trawls, the first-hand observational data obtained from ROV or manned submersible dives is valid and more informative. For example, upon observation of a benthic habitat, certain environmental conditions (eg currents, nutrients, sediment mixing etc) can be noted and may even help to explain the presence / absence of certain species within a habitat (Trenkel *et al.*, 2004). None of this information could be known from trawl-derived data.

What is a Deep-Water Coral Reef?

Coral reefs that this review is concerned with are constructed by colonies of Scleractinian (reef-building) stony corals. As these coral polyps grow they deposit a calcareous skeleton and it is this that forms the reef structure (Roberts *et al.*, 2006). The known types of cold-water scleractinian corals include *Lophelia pertusa*, *Madrepora oculata*, *Goniocorella dumosa*, *Oculina varicosa*, *Enallopsammia profunda* and *Solenosmilia variabilis* (Freiwald *et al.*, 2004). Of these, *Lophelia pertusa* is probably the most studied, and covers a large geographical range (Freiwald *et al.*, 2004; Costello *et al.*, 2005; Husebø *et al.*, 2002).

The present review aims to ascertain our current understanding of deep-water coral reefs in terms of their worldwide distribution, faunal ecology and any anthropogenic impacts upon these unique habitats. This review defines a deep-water coral reef as being more than 100m depth. Therefore, those found in the cold, current swept fjords are excluded from this review; as are any other cold-water coral reefs occurring shallower than 100m.

Distribution

Deep-water coral reefs have a cosmopolitan distribution, occurring in all ocean basins (Guinotte *et al.*, 2006), on areas of the seabed with certain rugged topographies such as continental shelves and slopes, seamounts and oceanic banks (for exact locations, see appropriate references from Freiwald *et al.*, 2004). They have also been observed to inhabit the artificial structures of oil and gas platforms (Gas & Roberts, 2006) and shipwrecks (Costello *et al.*, 2005). Though scientific study of deep-water coral reefs is limited, it is known that corals require hard substrate for attachment, together with a surrounding temperature between 4^oC and 12^oC (Roberts *et al.*, 2006).

Deep-water coral reefs are found in current swept areas of the seabed. This is because whereas corals of shallow, tropical waters rely on the photosynthetic products of their symbiotic algae for nutrition, deep-water corals are azooxanthellate (lack symbiotic algae) filter-feeders, relying upon currents to supply them with nutrition. Furthermore, currents minimise sediment deposition on the coral reefs. This is also beneficial to the corals as sediment build-up can fatally damage these fragile feeding tentacles.

Little is known in scientific literature about the reproductive biology of deep-water corals. Van Soest *et al* (2007) assumes that they must have a planktonic larval stage reminiscent of shallow water coral reefs. Gas and Roberts (2006) are in agreement with this and say that the fact no *Lophelia pertusa* corals were found in the North Sea before the introduction (and subsequent colonisation) of oil and gas platforms (providing hard substrata) is proof of a planktonic larva stage (see also Fossa *et al.*, 2002). However, without further investigation, the theory of reproduction via broadcast spawning in deep-water corals remains purely an assumption (Burgess & Babcock, 2005).

Furthermore, recent studies have related the abundance of deep-water scleractinian corals to the depth of the Aragonite Saturation Horizon (ASH). Aragonite is the form of calcium carbonate required by corals to build their skeletons, and therefore needs to be available in the surrounding water. Thus, Guinotte *et al* (2006) attributed (at least in part) the high abundance of deep-water scleractinian corals in the North Atlantic to its deep (>2km) ASH, and likewise the octocoral and stylasterid (soft corals, non-reef building) dominated North Pacific to its much shallower (50-600m) ASH. The few scleractinian corals observed in the North Pacific tended to be solitary as opposed to reef-forming, supporting this hypothesis.

There is much debate in scientific literature as to whether or not the formation of deep-water coral reefs relies upon hydrocarbon seepage from the seafloor. Lindberg *et al* (2007) notes the presence of pockmarks next to deep-water coral reefs, which they speculate as being most likely caused by expulsion of biogenic gas from the seafloor. Overall, the findings of Lindberg *et al*'s study agree with Hovland and Risk's (2003) review: although some evidence of a relationship between the locations of some deep-water coral reefs and possible hydrocarbon seeps exists, most if not all of the evidence is merely circumstantial. Recent studies (reviewed by Roberts *et al*, 2006) have now found that deep-water corals rely on surface primary production and its subsequent transport to the seafloor (Roberts *et al*, 2006; Guinotte *et al.*, 2006).

As new technologies (including sonar mapping, ROV and manned submersible use) are developed and become more widespread, further study of the requirements of deep-water corals for settlement, growth and nutrition needs to be undertaken. Indeed, Ross & Quattrini (2007) notes the true difficulties in obtaining all the physiochemical attributes of an area of the deep-sea.

Ecology

Cold-water coral reefs are a habitat comprised of scleractinian (reef-building) corals. Home to a diverse assemblage of associated organisms it provides a 3D structure in an otherwise largely flat, empty expanse (Costello *et al.*, 2005). Even with the relatively little amount of knowledge held about deep-water coral reefs, it is thought they are true rivals of the better understood and highly biodiverse shallow water coral reefs, at least in terms of faunal diversity (Van Soest *et al.*, 2007).

Coral

As filter feeders, the most likely food source for deep-water corals is a mix of plankton and particulate organic matter (Freiwald *et al.*, 2004). Phytodetritus, from productive surface waters, falls through the water column and the benthic boundary layer (via Ekman transport) to be trapped by deep-water coral mounds. The fact that deep-water coral reefs usually occur beneath surface waters of high primary production, demonstrates how this suspended phytodetritus is an important nutritional source for these corals (Guinotte *et al.*, 2006; Mienis *et al.*, 2007). Mortensen's (2001) aquaria observations of *Lophelia pertusa* polyps preying upon zooplankton, may be the only true first-hand observation (or one of very few). Therefore, more first-hand study needs to be undertaken in this area.

Predation and parasitism of deep-water corals also remains to be thoroughly investigated. The UNEP report of 2004 (Freiwald *et al.*, 2004) states that no predation upon deep-water coral reefs has been documented, thus far. It goes on to say how even though nearly all echinoderm groups have been observed in many cold-water coral reef ecosystems, but none have been observed grazing on deep-water scleractinian corals. This claim may be incorrect as they include a picture of an unidentified starfish clearly wrapped around a branch of *Lophelia*.

The UNEP report (Freiwald *et al.*, 2004) cites numerous scientific references regarding organisms that have been observed to parasitise Scleractinian corals (also Octocorals and Styliasterid 'lace' corals). These parasites include ascothoracid and copepod crustaceans, and the foraminifer *Hyrrokkia sarcophagi*, the latter being able to burrow straight through the calcareous skeleton of the host coral (Freiwald & Schönfeld, 1996). Any effects of either parasitism or predation upon deep-water coral reefs still remain to be explored, even though Freiwald & Schönfeld declared the need for this research to be undertaken over a decade ago.

In Atlantic waters, the polychaete worm *Eunice norvegica*, has been found to have a mutualistic symbiotic relationship with *Lophelia pertusa* coral reefs (Gas & Roberts, 2006). The polychaete can burrow into the calcareous skeleton of the coral, making its home within. Mortensen (2001) observed that *E.norvegica* took food particles collected by the host coral polyps for its own, cleared sediment from the coral and stimulated the host coral to surround its parchment tube with its calcareous skeleton as a result of its own tube-building process. Roberts (2005) also noted its ability to aggregate portions of the reef framework, thereby enhancing reef growth.

Deep-Water Coral Reefs as Fish Habitat

Deep-sea coral reefs provide a 3D habitat for a diverse range of fish and invertebrates (Costello *et al.*, 2005) in an otherwise largely flat, empty expanse. Many studies have recorded observations of fish aggregating around/in deep-water coral reef habitat. Furthermore, Husebø *et al.*'s (2002) study found significantly more fish in coral habitats than non-coral habitats. Although the precise importance of cold-water coral reefs to fish has not as yet been truly elucidated, recent research (using ROVs and manned submersibles) points towards it offering protection from predation, a suitable feeding grounds and a nursery habitat for juvenile fishes.

Many recent studies have recorded the redfish *Sebastes spp* to be associated with deep-water coral reefs. Usually observed to be stationary (e.g. Costello *et al.*, 2005 and Fosså *et al.*, 2002), Husebø *et al.* (2002) also observed *Sebastes* swimming slowly over the reef. *Sebastes spp* have also been observed associated with shipwrecks where they display this same, stationary position (Costello *et al.*, 2005; Husebø *et al.*, 2002: observations of a Norwegian coastguard). Husebø *et al.* (2002) surmises that it may well be the physical structures offered by shipwrecks and deep-water coral reefs that is appealing to the redfish, perhaps affording it some protection from predation. This is in accordance with Costello *et al.*'s (2005) later speculation that *Sebastes* uses wrecks and coral reefs for the same purpose. Indeed, Fosså (in Husebø *et al.*, 2002: personal observation) and Costello *et al.* (2005) observed *Sebastes* both hiding in a deep-water coral reef, and showing the disturbance behaviour of swimming away to hide by the reef upon approach of the ROV. These findings also correlate with the idea of a physical structure being used by *Sebastes* as protection.

Deep-water coral reefs provide a plethora of food for many associated benthic organisms (Costello *et al.*, 2005). The aforementioned high abundance of zooplankton in a deep-water coral reef habitat is a direct food source for zooplanktivorous fish such as *Sebastes* (Husebø *et al.*, 2002), and many associated crustaceans. An example of the latter would be Hudson and Wigham's (2003) observation of the squat lobster *Munida sarsi* preying upon krill (which Ross & Quattrini (2007) noted was in a much higher density around coral habitats than non-coral habitats). Moreover, Husebø *et al.* (2002) and Bergstad (1991) both found that Ling and Tusk feed primarily on smaller fish and various crustacea (eg *Munida spp*). Therefore, the possible reason for these fish spp (at least) to be commonly found associated with deep-water coral reef habitats may be due to their feeding habits (Husebø *et al.*, 2002). In this way, deep-water coral reefs also contribute to the trophic dynamics of the reef and its associated fauna. Indeed, Husebø *et al.* (2002) not only discovered that benthic ichthyofauna associated with deep-water coral reefs tend to feed on what is available in the coral habitat, but that they are also able to adjust their diet accordingly.

There is some evidence that deep-water coral reefs are used as a protective nursery habitat for juvenile fishes. During the spawning months of May and June, pregnant *Sebastes* were observed in deep-water coral reef habitat (Fosså *et al.*, 2002; Costello *et al.*, 2005). Though there has not been any record of eggs from obligate deep-water coral reef fish, *Raja* ray eggs have been observed within a deep-water coral habitat by Fosså *et al.* (2002). The fact that the presence of juvenile fishes has not yet been documented in scientific literature does not necessarily mean they are not there. As M.J. Costello notes (personal observations, in: Costello *et al.*, 2005), with such a complex and little studied habitat as a deep-water coral reef, smaller (i.e. juvenile) fish are much more difficult to notice, especially with the larger fish present. Another reason may be the difficulty in discerning different size groups of fish upon observation of this habitat.

Other Associated Fauna

In scientific literature, fish are clearly the best studied of the deep-water coral reef fauna. This is likely to be due to the fact, as Van Soest *et al* (2007) suggests, researchers are usually more inclined to look for megafauna (such as large fish) which are much easier to spot than smaller, more cryptic species. Furevik *et al* (cited in Husebø *et al.*, 2002) observed the other most abundant macrofauna of a deep-water coral reef to include Hexactinellid sponges, gorgonians (*Paramuricea placomus*, *Paragorgia arborea* and *Primnoa*), soft corals (*Capnella* sp.), squat lobsters (*Munida* spp.), crabs (*Lithodes* sp.), sea urchins (*Cidaris cidaris*) and ophiuroid starfish. Information concerning their ecology is very limited.

Van Soest *et al* (2007) remarks how sponges (eg *Hexadella dedritifera*) have an important role within deep-water coral reefs being home to microsymbiont communities, as filter feeders, and excavating agents. However, they admit that none of these ecological interactions have yet been studied in nearly enough detail as to discover and exactly what these relationships are (eg if sponges compete for space on the reef with coral, the main reef filter-feeders).

With the rate and number of newly discovered deep-water coral reefs ever-increasing, their true importance as habitats for fish and invertebrates can not as yet be fully appreciated (Costello *et al.*, 2005).

Anthropogenic Impacts

Humans are having an adverse effect upon the fragile habitat of deep-water coral reefs, both directly and indirectly. Deep-water coral grows extremely slowly. Infact, *Lophelia pertusa* has been estimated to take hundreds of year to attain a diameter of just 1.5-2 metres (Fosså *et al.*, 2002). Moreover, some deep-water coral reefs have been estimated to be up to 8,000 years old (Costello *et al.*, 2005). The destruction of such ancient, slowly growing and unique habitats will surely result in a decrease in biodiversity of the associated fauna as well as the habitat.

Trawling

Additional to the ecological consequences of destroying habitat, there are economical implications too. For example, many studies have found commercially important fish (eg tusk (*Brosme brosme*) and ling (*Molva molva*) to be associated with deep-water coral reefs (eg Husebø *et al.*, 2002; Hall-Spencer *et al.*, 2002). With a significant decrease in their habitat, it is logical to expect a decline in the abundance of these fish to follow as Costello *et al* (2005) notes there is no evidence of any suitable alternative habitat for these fish at the depths where *Lophelia* reefs are found. Indeed, the recent decline in catch of tusk and ling that Husebø *et al* (2002) reports, may well be explained by the prior decrease in deep-water coral habitat due to intense past trawling of the area for fish.

There are numerous bans and conservation measures now being put into place with the aim of conserving deep-water coral reefs because their importance as habitat for (especially) fishes and invertebrates is becoming clearer as more benthic studies are undertaken. (For an overview of some of these conservation measures, see: Freiwald *et al* (2004).)

Global Warming

Global warming (the result of anthropogenic increase in CO₂ release into the atmosphere) is an ever-increasing issue in the world of today. Though numerous studies have been undertaken with the aim to discover how shallow-water corals will be affected by a future temperature rise, little study has been done concerning deep-water corals. Guinotte *et al* (2006) postulates that a future rise in atmospheric CO₂ will lower the pH of the oceans, causing a decrease in available aragonite that coral use to form their reef structures. They go on to estimate that the resulting shallower ASH will affect the distribution of deep-water coral reefs, perhaps leading to great losses in this habitat.

Conclusions

With so much still unknown about such a biologically and economically important habitat as deep-water coral reefs, it is imperative more research is done, with the aims of better understanding and conserving these biological hotspots, before human activities destroy them beyond their revival threshold.

Currently, as outlined throughout this review, our gaps in knowledge concerning deep-water coral reefs are cavernous:

- What is the reproductive biology of deep-water corals? Do they reproduce via broadcast spawning of planktonic larvae as shallow-water corals are known to?
- Where are there more as yet undiscovered deep-water coral reefs? Are they limited by the same environmental conditions that scientists believe?
- What are the between-species differences of deep-water corals in terms of biology, ecology and environmental constraints?

Lack of detailed prior knowledge about the ecology of deep-sea coral reefs has restricted our ability to infer ecosystem functions, reasoning behind any observed habitat associations and how habitat complexity contributes to the ecology of deep-water coral reef habitats (Ross & Quattrini, 2007). Therefore, further studies into these coral habitat associations of fish, crustacea and infauna need to be undertaken. It will only be from ongoing research into these relatively unknown habitats, that we can gain an appreciation of their ecological and economical importance, or their true need for conservation.

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