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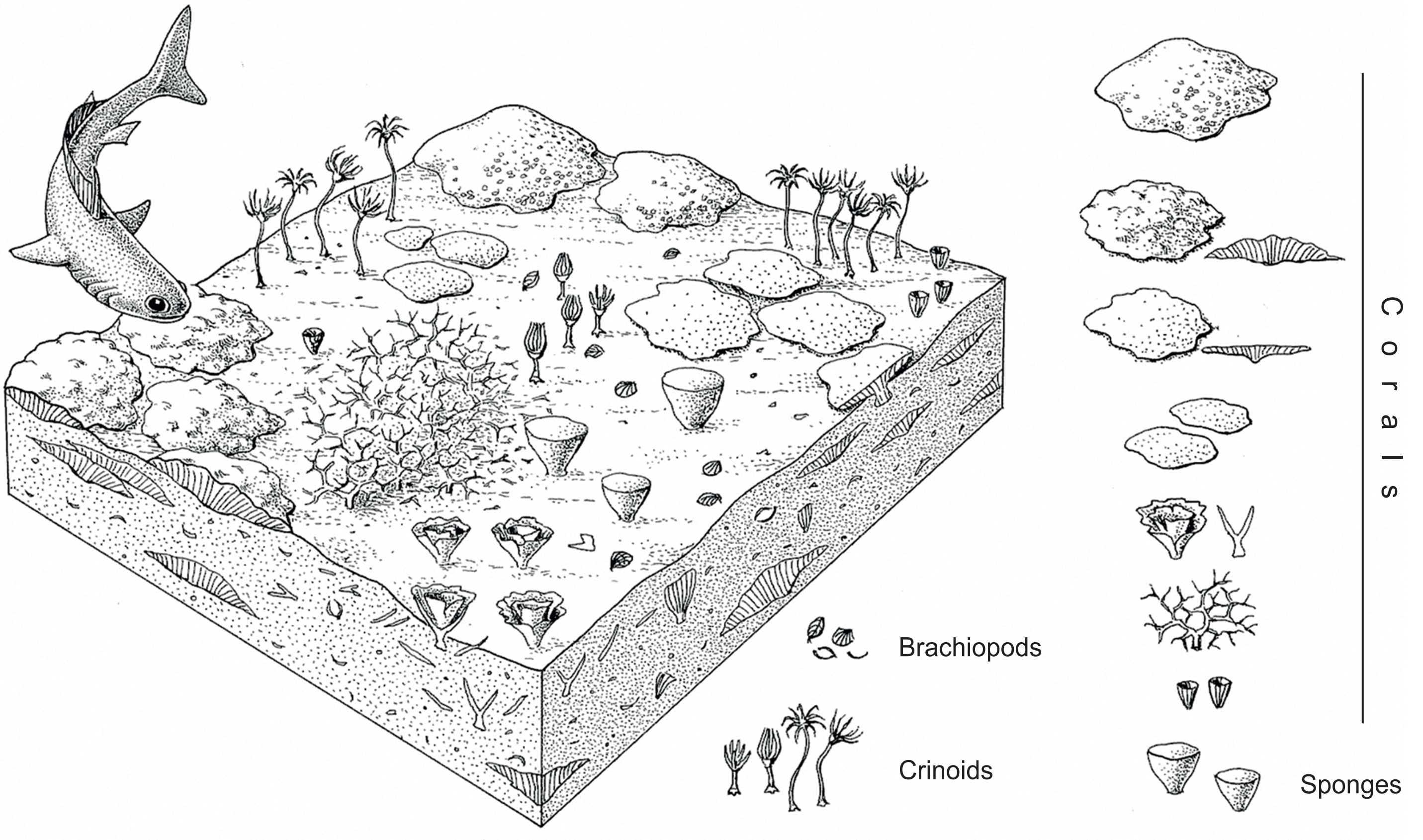
Reefs in the Twilight Zone

Coral reefs, commonly found in tropical coastal areas, are the world's most complex marine ecosystems. But how do deeper-water corals differ from easier-to-study reefs in shallower waters?

Mesophotic coral reef survey with disc-shaped ("platy") coral colonies visible in the foreground

DR PIM BONGAERTS



Reconstruction of a Devonian mesophotic reef from the Holy Cross Mountains with flat and foliose corals and crinoids (taken from Zapalski M. et al., *Coral Reefs* 2017). Drawing by B. Waksmundzki

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Coral reefs play an extremely important role: despite occupying merely 0.01% of the ocean floor, they provide habitats for nearly 25% of all known marine animal species, and indeed 5% of all known species planet-wide.

Corals have been known since antiquity – they were mentioned by Theophrastus of Eresos (fourth century BC), but their nature remained completely unknown (Theophrastus classified them as minerals). A significant turning point in human understanding of the nature of corals came with the research of Luigi F. Marsigli of Bologna (also known as "Marsilius"). Using a primitive microscope, he observed living corals and described in detail their appearance and behavior (with "eight petals" and sensitivity to touch). Those observations and analysis of the smell of decaying corals (similar to that of cabbage) led him to the conclusion that corals should be considered plants (1625). Nearly a century later (1723), those studies led to another breakthrough, when Jean-André Peyssonnel, inspired by the work of Marsilius, conducted very similar research (but on a larger scale) and arrived at a different, yet correct conclusion: that corals are in fact animals. Carl Linnaeus had a lot of trouble classifying corals and, Peyssonnel's work notwithstanding, he classified them as plants.

Most corals known to early scholars came from shallow coastal waters. Little was known about corals living at greater depths, although Linnaeus and Charles Darwin (100 years later) did describe deep-water corals – the latter even described corals from a depth of 120 meters. Deep-water corals were retrieved sporadically and in most cases accidentally, but they were not studied systematically for a long time. Specimens were obtained during dredging (which involved dragging special containers along the seabed) or by the use of hooks, but there was an acute lack of observations of live animals at such depths. It was not until the 1950s and 1960s that scuba diving using compressed air began to gain popularity. For technical reasons, observations and studies of entire ecosystems focused on waters no deeper than 30 meters. Greater depths require better equipment, as well as different techniques and procedures. As a result of this research, it came to be assumed that the bathymetric range of corals was just 30 meters, and their occurrence below that depth was treated as incidental.

Symbiosis

Shallow-water corals build reefs in symbiosis with algae, chiefly dinoflagellates (such symbiotic corals are called "zooxanthellate"). The coral provides the algae with both shelter and carbon dioxide (as a waste product of respiration). The algae use the latter for more efficient photosynthesis, and shares the carbohydrates produced in this process with the coral. By using carbon dioxide, the algae also increase the alkalinity of the seawater surrounding the coral's skeleton, which translates into significantly faster skeleton growth. Consequently, reef-building corals are chiefly zooxanthellate species. Deep-water corals do not form symbiotic relationships with algae, as they live in environments that are not reached by sunlight. What, then, is the depth limit for zooxanthellate corals?

Exploration of the deep sea and the ocean floor has attracted researchers since the time of William Beebe, who dove to a depth of 923 meters in a vessel called the Bathysphere in 1934. The diverse forms of deep-sea creatures (including ones that glowed, had appendages or expandable stomachs) attracted great interest, which translated into funding for research. As a result, there came to be a certain gap in the study of marine ecosystems: the relatively well-studied reefs were those at depths of up to 30 meters and those in the deep sea, where no light breaks through. Everything between those two areas was a kind of "twilight zone" – both literally and figuratively.

Cross sections of platy mesophotic corals from the Wee Jasper site, New South Wales, Australia

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A turning point in the exploration of this twilight zone came as a result of a number of technological improvements that permitted divers to descend down below 30 meters (called "technical diving") – consequently, dives conducted even 100 meters below the surface or lower became quite common. One such invention was "rebreathers," or closed-circuit devices that allowed carbon dioxide to be absorbed from the air exhaled by the diver, which could then be enriched with oxygen and reused. All this made it possible to perform deeper and longer dives. The twenty-first century also witnessed the rise of remotely operated vehicles (ROVs) – underwater robots which made it possible to more conveniently explore the deep sea at shallower depths.

As a result of these and other inventions, exploration of the twilight zone gained momentum in the 1980s. Zooxanthellate corals turned out to inhabit waters down to depths of about 170 meters (which is how far the light needed for photosynthesis penetrates into the sea). At such depths, they form what are called mesophotic reefs (from the Latin words *meso* and *photic*, meaning "middle" and "light") – in other words, those in the "twilight zone." Back in the 1980s, there were one or two publications devoted to such ecosystems per year, but more recently, their number has come to exceed 400 per year. Around 2010, researchers realized that, all told, mesophotic reefs probably cover larger areas of the ocean floor than their shallow-water counterparts.

Light

Living in an environment with depleted sunlight, where every quantum of solar energy matters, requires special adaptations. Zooxanthellate corals adapt to the conditions at greater depths chiefly by developing significantly flatter skeletons, which form a structure resembling solar panels to facilitate sunlight exposure to the tissues that contain symbiotic algae. The same coral species may be almost spherical in shape in shallow waters (these are called massive colonies), but display a disc-shaped ("platy") or leaf-shaped ("foliose") morphology in the deep sea. Importantly, such adaptations certainly did not occur suddenly – they must have resulted from long natural selection, so we may be tempted to look for evidence of the existence of such ecosystems in the geological past. In this, we are significantly aided by the fact that coral skeletons are made of calcium carbonate, so they are well-preserved in the fossil record.

In 2000, the British researcher Brian R. Rosen and his colleagues were the first to identify mesophotic corals in the fissil record. They concluded that the first ecosystems formed by these organisms had arisen in the Late Triassic. Later studies (including those conducted by the team led by Prof. Bogusław Kołodziej of the Jagiellonian University) revealed the presence of mesophotic ecosystems in the Middle Triassic (about 245 million years ago). The period was characterized by the expansion of the sixfold-symmetrical hexacorallia (Scleractinia) corals, so the emergence of mesophotic coral ecosystems (MCEs) is close in time to the appearance of reefs built by scleractinian corals.

Reefs built by corals also existed in the Paleozoic Era (541–250 million years ago). Reefs from the Middle Devonian (about 380 million years ago) were close in size to modern ones, but they were built by different groups of coral species. The corals of the Paleozoic, called tabulate corals and rugose corals, died out in the Permian–Triassic extinction event and most likely left no descendants. We know very little about their physiology, somewhat more about their ecology.

The structure resembling "solar panels" exhibited by modern Scleractinia corals follows from simple laws of physics. If an organism wants to harvest light, it will develop structures helping it achieve this goal. An analysis of various Paleozoic coral communities has revealed several groups considered to have been mesophotic. The first such finds came from Middle Devonian rocks from Poland's Holy Cross Mountains (nearly 390 million years ago), followed by further finds from Silurian sediments from Gotland in Sweden (roughly 430 million years ago) and Devonian sediments in Morocco.

Coral assemblages from Devonian rocks, extracted in the Laskowa Quarry near Kielce, Poland, have been known for a long time. It was more or less obvious what they looked like, but their flat shape did not attract separate attention in previous research. This assemblage was only identified as typically mesophotic, dominated by platy or foliose corals with a large share of branching forms, after an analysis of coral shapes (and not their species composition) combined with sedimentological analysis. This year, we carried out a study of very similar and slightly older assemblages in New South Wales (Australia). The Wee Jasper site there has long been known for the presence of perfectly preserved placoderms, and our research focused on the layers that contained corals. This is the first known complete reef ecosystem with a well-developed fauna of fish, which are an extremely important component of the ecosystem in today's reefs.

Murky waters

Not every coral assemblage with flat skeletons is mesophotic, however. The kind of skeletal morphology described here is related to sunlight availability, not to depth per se. Studies of modern corals off the coast of Florida have shown that mesophotic-like skeletons can appear in turbid waters already at the depth of around 10 meters. Some researchers divide twilight-zone (mesophotic) reefs into "blue-water" reefs and "brown-water" reefs. The former are true mesophotic reefs, found in deep clear waters, where the platy (disc-shaped) form of coral colonies is conditioned by the light absorption by seawater.

Brown-water mesophotic reefs are coral assemblages found in turbid and shallow waters, where light gets absorbed by sediment particles dispersed in water. Such reefs are commonly found, for example, in offshore shelf areas of the Great Barrier Reef. A Polish-Australian study of the Middle Devonian corals from the Australian state of Queensland (as part of the present author's ongoing grant-funded project) showed that mesophotic brown-water reefs also existed in the Paleozoic. They were characterized by a large share of platy corals, but branching and massive forms were also abundant (whereas the latter are practically absent from blue-water mesophotic ecosystems).

Climate change in the twenty-first century poses a major threat to coral reefs. Nevertheless, it remains unclear to what extent this danger also applies to mesophotic reefs. Might they serve as a refugium for shallow-water reef species? Unfortunately, our knowledge of such ecosystems and their geological history is still very fragmentary. Modern reef ecosystems are relatively well-studied only in areas near major research centers (for example in Hawaii and the Great Barrier Reef in Australia). However, we know too little to hazard consistent generalizations about the factors controlling the development of these reefs or the distribution of coral species, which makes it difficult to identify the threats. This makes further study of mesophotic reefs all the more worthwhile. ■

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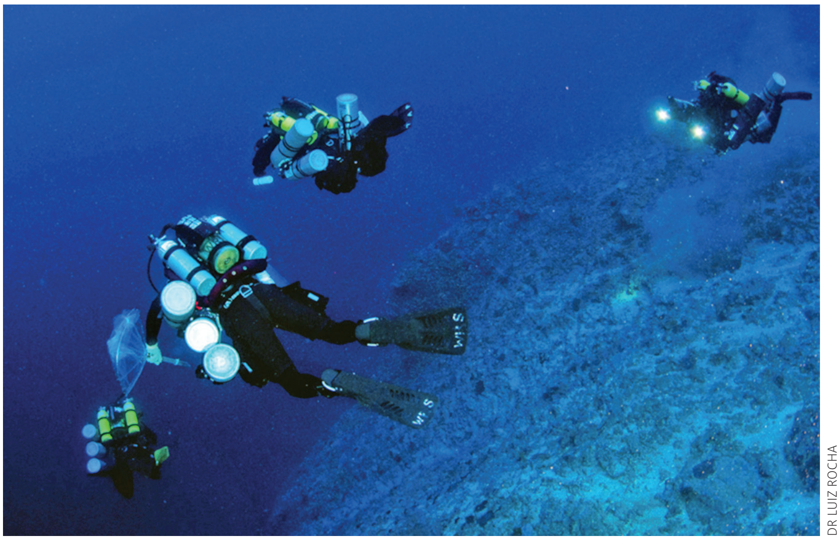

DR LUIZ ROCHA

Researchers from the California Academy of Sciences conducting a deep-water dive to study the mesophotic coral reef of Mo'orea, French Polynesia. Use of multiple tanks is typical of technical diving

Further reading:

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