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Coral-reef area and the contributions of reefs to processes and resources of the world's oceans

Do coral reefs constitute a quantitatively significant ecosystem on a global scale? The area, calcium mass balance, and fisheries yield of reefs provide important geographical, geochemical and biological criteria for answering this question. After considering them, I conclude that coral reefs should not be overlooked in the quantitative assessment of global resources.

Menard and Smith[1] updated hypsographic data for the world's oceans, and Professor Menard has kindly provided me with a summary of the areas within depth increments tabulated by 10° 'square' of latitude and longitude. The shallowest depth increment in that summary is 0-200 m. Wells[2] presented a map of the global distribution of coral reefs, updating earlier work. Wells' map was used to estimate visually (to the nearest 25%) the percentage of coastline and other shoals fronted by reefs within each 10° square. Menard and Smith's tabulation was used to determine the total area shallower than 200 m within those squares having reefs. I assumed that water depth is evenly distributed between 0 and 200 m and that along those coasts having reefs they extend from 0 to an average of 30 m water depth. Coral communities can extend well below 30 m, so this analysis should be conservative. Reef area within each square is thus estimated to be the product of 15% of the 0-200 m area times the proportion of shoal area with reefs.

This assessment of reef area includes not only the wave-resistant framework created by corals, coralline algae and other cementing organisms but also associated, contiguous and predominantly soft-bottom biological communities and sedimentary assemblages.

Table 1 summarises the results. Total reef area estimated according to this procedure is approximately 6×10^5 km², over half of which is in the Asiatic Mediterranean and Indian Oceans (see Fig. 1 and ref. 1 for the ocean boundaries used). As determined by comparison with the global hypsographic data[1], reefs constitute about 0.17% of the world ocean area and about 15% of the shallow sea floor within the 0-30 m depth range. Newell[3] used earlier maps, arrived (by a method not explained in his text) at a global reef area of 1.5×10^6 km², and arbitrarily divided his estimates by 10. The average of his upper and lower area estimates is close to my estimate.

Calcification is obviously a major biogeochemical process on coral reefs, and a moderate amount is known about the $CaCO_3$ production rate of reefs. Comparison of the amount of $CaCO_3$ precipitated by reefs with the calcium input to the oceans provides a measure of the role of reefs in the world calcium balance. Many reef environments calcify at one of two characteristic rates[4,5]. A production rate of about 8 mol $CaCO_3$ m^{-2} yr^{-1} prevails over regionally extensive areas, whereas more localised and highly active portions of reefs calcify at 40 mol $CaCO_3$ m^{-2} yr^{-1}. By far the major proportional area of reefs calcifies relatively slowly (for example, lagoons, sand flats, and so on), although the observer's attention may focus on areas with a high rate of calcification (for example, coral thickets, algal pavements, and so on). I estimate that 90-95% of the global reef area calcifies at the 'slow rate' and the remainder at the 'fast rate'; then reefs precipitate about 6×10^{12} mol $CaCO_3$ annually. This estimate is likely to be conservative. The proportion of reefs which calcifies at the higher rate may be substantially larger than I have estimated, and some authors[6-8] believe that certain estimates[4] of the upper modal rate of reef calcification are low. (I have deliberately omitted estimates strictly of vertical accretion rates, because of problems in intercalibrating vertical accretion and mass accretion data.) The most serious potential for error in this estimate is therefore in an underestimate of reef calcification (that is, that the high production area or rate has been underestimated).

Table 1 Area covered by the world's coral reefs, by major oceanic region

Oceanic region (abbreviation on Fig. 1)	Reef area ($\times$1,000 km²)	% Total reef area
Asiatic Mediterranean (ASM.)	182	30
Indian (IND.)	146	24
South Pacific (S. PAC.)	77	13
North Pacific (N. PAC.)	76	12
Caribbean (CARIB.)	57	9
North Atlantic (N. ATL.)	32	5
Red Sea (RED)	27	4
Persian Gulf (PER.)	12	2
South Atlantic (S. ATL.)	8	1
Total	617	100

The delivery of calcium to the world's oceans is about 1.2×10^{13} mol yr^{-1} (ref. 9). Thus, reef production at least temporarily precipitates an amount of calcium equivalent to about 50% of the input. By the very construction of wave-resistant structures and sediment-trapping lagoons, reefs can be expected to retain a substantial fraction of their sedimentary products and to minimise dissolution. The quantitative importance of such re-solution remains unknown, but it seems clear that reef sediments constitute a quantitatively significant global sink for calcium.

Reef fisheries potential provides yet another indicator of the quantitative significance of coral reefs. It has been suggested that the potential of reef fisheries may be substantially larger than has generally been appreciated, because of operational problems in utilising that potential[10]. The reef fisheries of the Caribbean Sea and Western North Atlantic Ocean have been examined in some detail; the potential yield of demersal fishes from reefs and adjacent deep shelf areas has been estimated to be 8×10^8 kg yr^{-1} (ref. 11). I assume that the demersal fishes from deep shelf areas should be included with the reef fishes themselves in evaluating potential reef yield, because these deep shelf demersal fishes probably derive much of their nutrition from the reefs.

The Caribbean plus North Atlantic reefs comprise 14% of the world's reefs (Table 1). If one can validly extrapolate

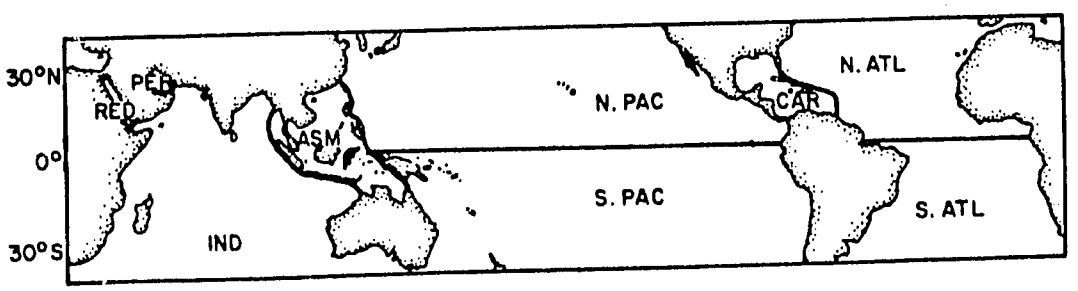

Fig. 1 Boundaries of oceanic provinces as used to evaluate reef areas.

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from the fisheries potential of that area to the world's reefs, then world reef fisheries potential is about 6×10^{9} kg yr^{-1}. The present commercial oceanic fish landings are about 7×10^{10} kg yr^{-1} (ref. 12); reef-related fisheries apparently have a potential yield near 9% of this total. Data are insufficient to establish what fraction of the reef fisheries potential is presently realised. Nor is it obvious to what extent subsistence fisheries excluded from the commercial landings might alter the importance of the reef fisheries potential.

These inventories are speculative and incomplete; nevertheless, they are sufficient to demonstrate that coral reefs are indeed a quantitatively significant ecosystem on a global scale.

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Production of methane and carbon dioxoue from methane thiol and dimethyl sulphide by anaerobic lake sediments

METHANE THIOL (methyl mercaptan, MeSH), its oxidation product, dimethyl disulphide (DMDS), and dimethyl sulphide (DMS) are naturally occurring metabolites. They are also produced by paper mills using the kraft pulp process[1] and cause an industrial odour problem because of their low odour threshold. Although the biological production of these compounds is fairly well understood[2], little is known about their biological decomposition. We report here that microbial populations present in anaerobic freshwater sediments and in anaerobic sewage digestor sludge are capable of metabolising the carbon in these volatile organic sulphur compounds to methane and carbon dioxide. Therefore, anaerobic habitats may serve as sinks in the biogeochemical cycling of these compounds.

MeSH and DMDS are produced from the methiol group of methionine by both aerobic and anaerobic microorganisms[2]. DMS is usually a minor product of methionine breakdown, and is more often produced from sulphonium compounds, such as the thetins found in algae and fungi[3]. Lovelock *et al.*[4] detected DMS in ocean waters and in the atmosphere over soils and have suggested that DMS plays a major role in the atmospheric sulphur cycle, but further studies are needed before the role of DMS can be ascertained.

In our studies of anaerobic metabolism of methionine by Lake Mendota (Wisconsin) sediments using low levels of radiolabelled methionine, we have obtained evidence that MeSH was cleaved from methionine, and that this MeSH was subsequently metabolised to methane, carbon dioxide and hydrogen sulphide[5]. For this mechanism to be possible, the metabolism of MeSH to these products needed to be demonstrated. Also, because metabolism by anaerobic sediments may be an important sink for DMS, it was of interest to determine if similar products were formed from DMS. The degradation of these compounds by Lake Mendota sediments was followed using ^{14}C-labelled MeSH and DMS. (For details, see Fig. 1.)

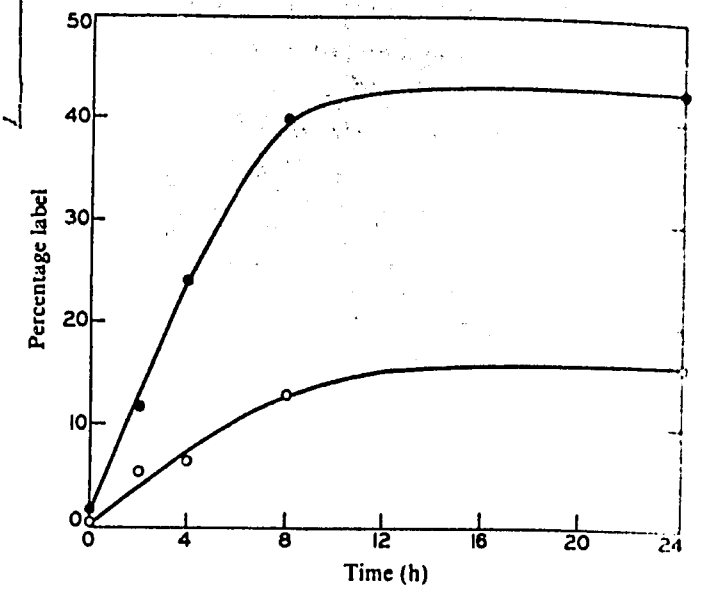

Fig. 1 Time course for ^{14}C-methane (●) and carbon dioxide production (○) from ^{14}C-labelled MeSH by Lake Mendota sediments. Five µl 1 M NaOH containing 2.2 nmol (250,000 d.p.m.) ^{14}C-labelled MeSH (New England Nuclear,) as the sodium mercaptide, was taken up into a Hamilton No. 701 10 µl syringe, and then 5 µl 1 M HCl was also taken up into the same syringe. This mixture was immediately injected through a neoprene serum septum into a 10ml serum vial containing 1 ml lake sediment in a nitrogen atmosphere. Thus, the solution injected was ^{14}C-MeSH in 10 µl 1 M NaCl. The sediments were mixed with a vortex mixer and incubated at 15 °C, the highest *in situ* temperature reached by the sediments. Preliminary experiments showed that the ^{14}C-MeSH was rapidly absorbed by the sediment, although some was also absorbed into the neoprene septum. The neoprene septum was necessary to keep the sediments anaerobic. Production of ^{14}C-labelled methane and carbon dioxide was followed using the gas chromatographic-proportion counter method of Nelson and Zeikus[6].

As shown in Fig. 1, ^{14}C-MeSH was rapidly metabolised to methane and carbon dioxide by the lake sediments. The ratio of methane to carbon dioxide produced is close to the 3 : 1 ratio predicted if MeSH was fermented in the manner predicted by the equation:

$$4CH_3SH + 3\,H_2O \rightarrow 3\,CH_4 + HCO_3^- + 4\,H_2S + H^+$$

This is similar to methanol fermentation by *Methanosarcina barkeri*[7].

One indication that a reaction is biological is that the reaction shows a temperature optimum. Figure 2 shows that MeSH metabolism showed a definite optimum at 37 °C, and there was essentially no activity at 55 °C. Although the 37 °C optimum is much higher than the maximum *in situ* temperature reached by the sediments (15 °C), it has been shown by Zeikus and Winfrey[8] that methanogenesis in Lake Mendota sediments has a similar optimum. At temperatures higher than 15 °C, the ratio between methane and CO_2 from MeSH increased, possibly due to a shift in metabolism caused by increased hydrogen production by sediment populations at these temperatures[9].

The effects of various additions on MeSH metabolism by sediments are presented in Table 1. Chloroform, a well-known inhibitor of one-carbon metabolism[10], when added to sediment at a fairly low concentration prevented all