Day 4: 23 Oct 2008, Thursday – Progress and Advances

Main Session
Grand Ballroom
Time: 15:20 – 15:40

Biogeochemical processes and water homeostasis in an ecologically purified captive marine ecosystem: facts and hypotheses

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Abstract

In nature, a number of positive and negative biogeochemical feedback loops interact to maintain the physicochemical properties of seawater in a dynamic meta-stable equilibrium. Recent findings have significantly improved the knowledge of these extremely complex mechanisms and by way of consequences have contributed to clarify the understanding of the functioning of ecological purification in captive marine ecosystems. Amongst these findings are: (a) the biogeochemical processes associated with the coastal filtration (the wave- and current-induced circulation of water and particles through the pores of shallow water permeable sediments); (b) the anaerobic oxidation of ammonium mediated by archaebacteria (a process called anammox); and (c) the activity of cryptic organisms, which inhabit the crevices of carbonate substrata. These latter organisms erode corals, shells as well as reef rocks, both chemically and mechanically, releasing chips and maintaining the alkalinity of water. Furthermore they recycle nutrients. In the light of these findings we draw the basis of a theoretical scheme, which supports the contention that biogeochemical processes can achieve a quasi-natural water homeostasis in an enclosed reef.

Introduction

Small ecologically balanced marine aquariums, set up by pioneering amateurs and naturalists, have existed a long time ago during the so-called Victorian Period. According to Taylor (1910), "*the first attempt to keep the seawater constantly fresh by the presence of seaweeds was successfully carried out by Mrs. Anna Thynne, in 1846*". Mrs. Anna Thynne was the wife of Lord John Thynne, the Sub-Dean of the Westminster Abbey. During several years, she kept in well-illuminated glass bowls live rocks and organisms collected from a tide pool and became "*the woman who brought the sea to the city*" (Stott, 2003). However, according to Lankester (1856) and Llyod (1876) N. B. Ward is the earliest recorded person who intentionally arranged together marine plants and animals so that they supported mutually and maintained the water pure.

The self-taught naturalist Philip Henry Gosse (1855) published the first handbook dealing with this simple technique. In the preface of this book Gosse writes: “*The increasing popularity of the Marine Aquarium demands a Handbook of Practical Instructions for establishing and maintaining it (…).* These sentences bear testimony that the Gosse’s previous books (Gosse, 1845 & 1854) had generated a wave of popular enthusiasm for naturally balanced aquaria. The technique that Gosse was explaining in the footprints of his predecessors consisted in imitating the chemistry of Nature by keeping marine invertebrates and fish in small tanks stocked with live sand and live rocks bearing seaweeds. One of the Gosse’s major prescriptions was the free access of sun’s rays to the plants (Gosse, 1855 page 10). Indeed he considered that the bubbles of pure oxygen released by the vegetation under the stimulus of light were “*the vivifying principle of animal life*”.

Yet in the middle of the 19th century, naturally balanced turnkey marine aquaria filled with artificial seawater (Figure 1) were sold in London. William Alford Lloyd, the man who designed the first public aquaria (Koob, 2004) in Paris (1860) and Hamburg (1864) owned the shop. In an advertisement put in the “Notes and Queries” of the Oxford Journals, December 6tn, 1856 (Figure 2), one can read: “*The discovery of a mode of readily making ARTIFICIAL SEA-WATER gives large facilities for the successful prosecution of the study. Much time, therefore, has been spent in assimilating it to the actual water of the ocean, so that it is now offered as an analytically correct compound, which thoroughly answers all purposes. Thus, the permanent maintenance of a collection of living Marine Animals and Algae in a state of domestication is rendered a far more easily attainable matter than even the cultivation of flowers. To render this yet more practicable in the hands of inexperienced persons, Mr. Lloyd makes it a point to keep in stock a number of small Portable Aquaria ready stocked, and with the balance of existence properly adjusted*.”

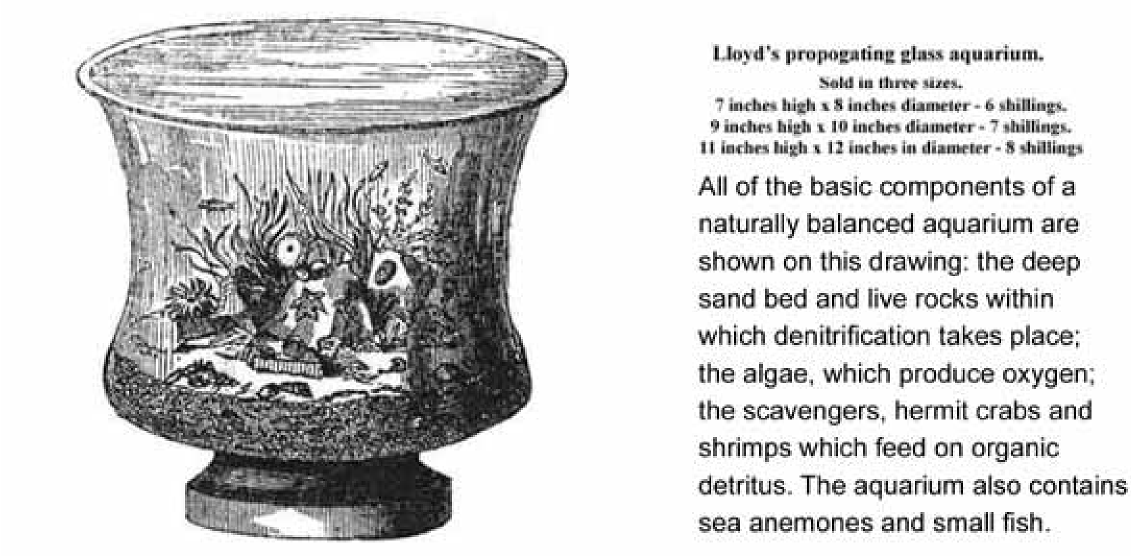

Figure 1. Aquarium sold in the Lloyds’ shop (from: www.parlouraquariums.org.uk)

THE MARINE AQUARIUM.

MR. W. ALFORD LLOYD begs to announce that he has REMOVED FROM ST. JOHN STREET ROAD, and that he has made very extensive arrangements for the SALE of LIVING MARINE ANIMALS, SEA-WEEDS, TANKS, and all the other accessories for the study of AQUARIUM NATURAL HISTORY.

MR. LLOYD'S Stock consists of Fifteen Thousand specimens, comprising Two Hundred genera, acclimated in Fifty large Plate-Glass Tanks, containing more than a Thousand Gallons of Sea-Water. The peculiarity which distinguishes this collection above that which any other single spot can furnish, and which renders it an object of attention not only to the amateur and student residing in London and in other inland places, but also to naturalists living at distant parts of the coast, is, that it is the result of an organized body of gatherers, posted at intervals in the richest localities; and thus our Marine Fauna and Flora are adequately represented in the Metropolis. The most delicate organizations can be packed to go safely by rail or by post.

The discovery of a mode of readily making ARTIFICIAL SEA-WATER gives large facilities for the successful prosecution of the study. Much time, therefore, has been spent in assimilating it to the actual water of the ocean, so that it is now offered as an analytically correct compound, which thoroughly answers all purposes. Thus, the permanent maintenance of a collection of living Marine Animals and Algæ in a state of domestication is rendered a far more easily attainable matter than even the cultivation of flowers. To render this yet more practicable in the hands of inexperienced persons, Mr. Lloyd makes it a point to keep in stock great numbers of small PORTABLE Aquaria ready stocked, and with the balance of existence properly adjusted.

Although from their nature the inhabitants of the Ocean have a greater interest than FRESH-WATER collections, the latter are duly provided, and various arrangements have been constructed so as to combine the Aquarium with the growth of Ferns, Mosses, Lichens, &c., and to adapt them for the study of the habits, embryology, and development of semi-aquatics, both animal and vegetable.

The Tanks are constructed by Messrs. Sanders & Woolcott (makers to the Zoological Society of London), to whom Mr. Lloyd is sole agent. These are not merely vessels for the reception of animals and plants, but a long series of observations as to the requirements demanded has so perfected them, that they very accurately imitate natural conditions, by attention being paid to the direction, intensity, and colour of the light employed; by the furnishing of various depths and densities of the water; by the regulation of the temperature; and by the arrangement of the whole for special purposes. Nor have the means of rendering them externally ornamental been neglected. As complete and independent pieces of furniture, many are mounted table-height, and are placed on castors, for the facility of being easily moved when full to any part of a room or house, as the aspect of the sun or the time of the year may demand.

*** A detailed List may be had on application.

W. ALFORD LLOYD, 19 and 20, Portland Road, Regent's Park, London.

Figure 2. Facsimile of the advertisement published in the "Notes and Queries" of the Oxford Journals in 1856 (from: http://nq.oxfordjournals.org/cgi/issue_pdf/backmatter_pdf/s2-II/49.pdf).

Verwey (1930) reports that the curators of the Onrust aquarium (built in 1928 in Indonesia) were using only live-rocks and full sunlight to keep corals and anemones.

In 1979, at the University of Nice, I have set up a coral reef microcosm by stocking a plenum-based 2,000-liters aquarium devoid of filter with live sand, live rocks, soft and hard corals as well as a number of other invertebrates and fish I had collected in the Red Sea (Jaubert 1981 & 1988). At the end of a maturation period of approximately 2 years this coral reef microcosm had reached a steady-state equilibrium and was as beautiful as a small Red Sea coral patch (Figure 3).

This microcosm has been thriving for 15 years without addition of calcium carbonate and with very few water changes. It would be likely still thriving today if I had not dismantled it when I moved full time to Monaco where I had established the European oceanographic center (Jaubert, *in the press*). The present paper aims to explain how biogeochemical processes may have interacted to achieve a quasi-perfect water homeostasis in this naturally balanced system.

Figure 3. Panoramic view of the coral reef microcosm shot in 1986 showing several major components of its population. Scleractinian Corals: *Acropora hemprichii* **(**Ehrenberg, 1834**),** *Acropora humilis* (Dana, 1846), *Favia favus* (Forsskål, 1775), *Favites pentagona* (Esper, 1794), *Fungia fungites* (Linnaeus, 1758), *Galaxea fascicularis* (Linnaeus, 1767), *Hydnophora exesa* (Pallas, 1766), *Lobophyllia corymbosa* (Forsskål, 1775), *Pavona cactus* (Forsskål, 1775), *Plerogyra sinuosa* (Dana, 1846), *Pocillopora verrucosa* (Ellis & Solander, 1786), *Seriatopora hystrix* (Dana, 1846), *Stylophora pistillata* (Esper, 1797), *Turbinaria mesenterina* (Lamarck, 1816). Alcyonarian corals: *Heteroxenia fuscescens* (Ehrenberg, 1834), *Litophyton arboreum* (Forsskål, 1775), *Sarcophyton glaucum* (Quoy & Gaimard, 1833), *Xenia macrospiculata* (Gohar, 1940). Mollusks: 2 large *Tridacna squamosa* (Lamark, 1819) and a number of *Stomatella auricula* (Lamarck, 1816). Echinoderms: 5 *Diadema setosum* (Leske, 1778). Fish: 1 *Acanthurus sohal* (Forsskål, 1776), 2 *Amphiprion bicinctus* (Rüppell, 1830) and their anemone *Heteractis crispa* (Hemprich & Ehremberg, 1834), 10 *Chromis viridis* (Cuvier, 1830), 12 *Dascyllus trimaculatus* (Rüppell, 1829), 1 *Pomacanthus asfur* (Forsskål, 1775), 3 *Pseudochromis fridmani* (Klauzewitz, 1968), 1 *Zebrasoma dejardinii* (Bennett, 1836). Additional information regarding the microcosm's set up can be found in Jaubert (1981; 1988 and in the press).

The fact that this above-described reef microcosm has been functioning for many years without water change and addition of calcium carbonate supports the contentions:

1. That the inputs and outputs of matter and energy were balanced;

2. That complex interactions involving photosynthesis, respiration, calcification and calcium carbonate dissolution were maintaining within "normal" limits the daily variations of the oxygen partial pressure (pO_2) and that of carbon dioxide (pCO_2) as well as those of the pH, the alkalinity, the aragonite saturation state (Ω_{arag}) and the equilibrium state between the different forms of dissolved inorganic carbon (DIC) of the water (Leclercq et al., 1999);

3. That nutrient removal and sequestration processes were enabling the system to maintain the oligotrophic conditions that corals needed to thrive.

The input of light energy and the microcosm's thermal balance

To meet the requirements of reef corals, the daylight, which illuminated the above-described microcosm, was complemented with the artificial light produced by 3 metal halide lamps switched on 12 hours a day. A large part of the light energy absorbed by the system was converted into heat. Over a cycle of 24 hours this light-generated heat exceeded the losses by evaporation and convection. Consequently, a lab-made heat pump was used to maintain the variations of temperature within the range of 24 °C (for the night minimum) to 26 °C (for the day maximum).

The microcosm's food web

The primary production of the microcosm produced enough vegetal biomass to meet the food requirements of all of the herbivorous organisms and of several scavengers. Conversely, the secondary production did not meet the metabolic demand of the carnivorous organisms, especially that of the fishes. To fill this gap, food was added every day to the system.

This food fuels metabolic and biogeochemical processes, which consume oxygen and release carbon dioxide as well as inorganic nutrients (mostly reactive forms of nitrogen and phosphorus). Only a small part of these nutrients is converted into vegetal biomass. Consequently the fact that the system remained oligotrophic means that efficient mechanisms removed these nutrients.

Most of the nutrient production and removal mechanisms were taking place in the thick layer (80-100 mm) of coarse (1-4 mm) coral sand, which covered the floor of the microcosm and their efficiency was largely controlled by the stirring-induced pore-water circulation (Figure 4).

The microcosm's pore-water circulation and bio-catalytic mineralizing filtration

By increasing fluid exchanges between the sediment and the overlying water several fold relative to simple molecular diffusion (Huettel et al., 1996; Precht and Huettel, 2003) the pore-water circulation plays a key role in the uptake and incorporation of particles (unconsumed food, animal feces, vegetal debris etc.) into permeable sediments. By way of consequence this process accelerates the oxygen and nutrient dynamics in these sediments. Precht and Huettel (2003) and Precht et al. (2004) have shown that coastal sediments form a gigantic filter, which purifies water.

In a previous paper dealing with the same microcosm (Jaubert, 1989) I had underestimated the intensity and the role of the stirring-induced pore-water circulation and the adjective "confined" used to qualify the plenum water was inappropriate. This circulation, likely facilitated by the plenum, has multiple consequences. It prevents the deeper layers of the sediment from becoming completely anoxic and by way of consequence prevents toxic pockets of hydrogen sulfide from forming. Consequently, the stirring should be adjusted so as to keep the intensity of the pore-water circulation within limits compatible with the maintenance of hypoxic conditions in the plenum (average concentration of oxygen: 0.5 $mg.l^{-1}$). Indeed, by increasing turbulences and pressure oscillations at the sediment-water interface a strong stirring would cause too much water to infiltrate the sediment and would bring too much oxygen to the deeper layers of the sand bed, breaking or even stopping the work of the denitrifying bacteria. On the other hand, the stirring-induced pore-water circulation achieves some mechanical filtration, which contributes to maintaining water in a state of perfect clearness. But turning the microcosm's sand bed into a "bio-catalytic mineralizing filter", similar to that which functions in nature (Wild et al., 2004 & 2005), is likely the most important effect of this circulation. Extremely complex bio-catalytic processes and metabolic pathways mediate the biogeochemical processes responsible for this purification.

The cycling of carbonates

In the reef microcosm the cycling of carbonates is a very important issue. Stony corals and calcareous algae take up Ca^{2+} and inorganic carbon (HCO_3^- and/or CO_3^{2-} ions). Conversely organisms that bore the live rocks (Zundelevich et al., 2006) and the skeletons of live and dead corals (Londoño-Cruz et al., 2003; Tribollet and Golubic, 2005) release Ca^{2+} and inorganic carbon to the overlying water column. Other biogeochemical processes such as ammonification, infauna respiration and heterotrophic denitrification that take place into carbonate sediments (Figure 4) produce the same effect (Charpy-Roubaud et al., 1999; Leclercq et al., 2002; Yates and Halley, 2006). In our reef microcosm these antagonistic processes were balanced and maintained within "normal" limits the daily variations of the pH, the alkalinity, the aragonite saturation state and the equilibrium state between the different forms of dissolved inorganic carbon (DIC) of the water.

The nitrogen cycle

The nitrogen cycle is the most intimately associated with microbes of all of the biogeochemical cycles. In the past few years, the discovery of new microbes and new nitrogen cycling processes has resulted in important changes in the understanding of the global nitrogen cycle (Burgin and Hamilton, 2007; Christopher et al., 2007; Ward et al., 2007). These findings, schematically illustrated in Figure 4, may explain why the reactive nitrogen production and removal processes, which took place in the closed-circuit microcosm, and their coupling were enough efficient to maintain the oligotrophic conditions that reef-building corals need to thrive.

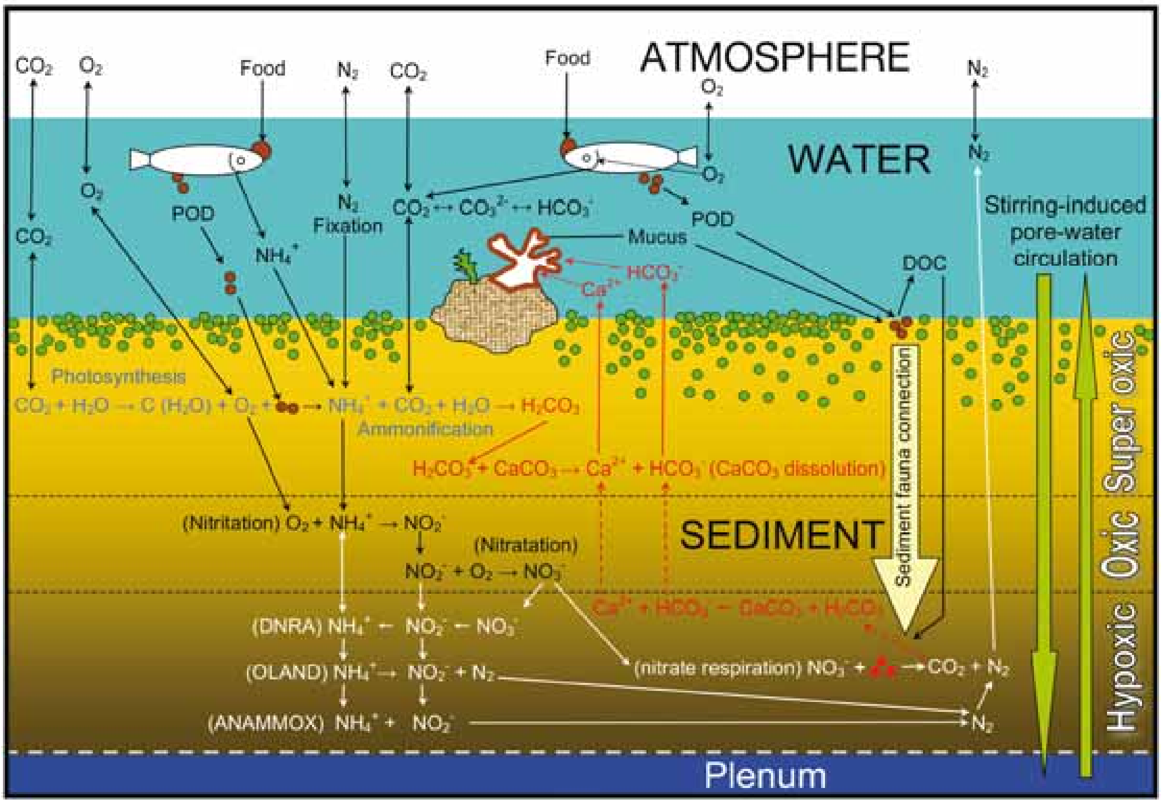

Figure 4. Schematic representation of the reactive nitrogen production and removal pathways and the correlated biogeochemical processes, which may take place in a plenum based microcosm. POD = Particulate Organic Detritus; DOC = Dissolved Organic Carbon; sediment micro-algae

New processes and players in the reactive nitrogen production and removal pathways

These new microbes are archaea. Some archaea mimic the processes completed by most of the classical bacteria. Several archaea bear the ammonia monooxygenase encoding genes (*amoA*). In shallow (300 m) marine waters and sediments the abundance of these Ammonia Oxidizing Archaea (AOA) is 1–2 orders of magnitude higher than that of the “classical” β- and γ-Proteobacteria (AOB), which were commonly thought to mediate nitrification in marine environments (Wuchter et al., 2006; Park et al., 2008). The respective roles of bacterial and archaeal nitrification are still debated. Other autotrophic archaea, which were unknown 10 years ago (Strous et al., 1998), carry out a specific process, the anaerobic oxidation of ammonium (anammox). According to Op den Camp et al. (2006) and Kuenen (2008) more than 50% of the molecular nitrogen lost by the Ocean would result from anammox reactions. Links with bacterial and archaeal nitritation may boost anammox (Lam et al., 2007). Anammox archaea have been found in almost all of the terrestrial and marine environments but not yet in reef sediments. Hence, they likely exist in a naturally balanced reef microcosm where they may participate with other microorganisms in the removal of the reactive forms of inorganic nitrogen. In permeable sediments, N_2 production rates from denitrification and anammox are up to 30 times higher in percolated zones than in those where there is no pore-water circulation (Gihring et al., 2008).

Schematic description of the microcosm's reactive nitrogen production and removal pathways

Figure 4 illustrates this description. During the day, the photosynthetic activity of the micro-algae (green spots) turns the upper layer of the sediment into a superoxic zone where heterotrophic bacteria find optimum conditions to mineralize Particulate Organic Detritus (POD) and release NH_4^+ and CO_2 (reaction in blue characters). This CO_2 hydrates and produces carbonic acid, which lowers the pore-water pH, corrodes the sand grains and releases calcium as well as bicarbonate ions (red characters). Pore-water circulation transfers these ions to the aquarium water where they replace those taken up by corals and algae. This process maintains the alkalinity and the aragonite saturation state in a steady-state equilibrium. On the other hand, nitrification, a 2 steps process (black characters) mediated by autotrophic bacteria and/or their archaeal counterparts oxidizes ammonium (NH_4^+) into nitrate (NO_3^-). The oxidation of NH_4^+ to NO_2^- releases protons (H^+), which lower the pore-water pH and facilitate $CaCO_3$ dissolution.

A series of nitrate-fueled processes (white characters) may take place in the sediment hypoxic zone and may interact to reduce NO_3^- ions to molecular nitrogen (N2). The heterotrophic denitrifying bacteria, which mediate denitrification, reduce the nitrate ions to molecular nitrogen to oxidize the organic carbon on which they feed. This carbon is derived from the detritus (POD) transferred from the water/sediment interface by the sediment fauna (white arrow) and from the Dissolved Organic Carbon (DOC) supplied by the stirring-induced pore-water circulation. The Dissimilatory Nitrate Reduction to Ammonium (DNRA) may reduce NO_3^- to NO_2^- and NH_4^+ (Kelly-Gerreyn et al., 2001). In nature, when it is coupled to anammox, this process may account for a significant fraction of the nitrogen loss of a system (Francis et al., 2007). The Oxygen-Limited Ammonium Nitrification-Denitrification (OLAND) is a 2 steps process (Valance-Harris, 2005), which can reduce NO_3^- to molecular nitrogen (N2). The NO_2^- produced by the first step of this process may fuel archaea-mediated anammox reactions (Van Hulle, 2005).

Phosphorus

Particulate (POP) and dissolved organic phosphorus (DOP) are mineralized into dissolved inorganic phosphorus (DIP). DIP is an essential chemical for life. In many marine environments it is a bio-limiting macronutrient because its availability is related to the insolubility of phosphate salts (Pratt, 2006). However, in aquaria opposite conditions tend to prevail. DOP and DIP are highly undesirable substances, which inhibit coral growth and promote blooms of cyanobacteria and algae. Since the microcosm never experienced such blooms during decades I presume that DIP was fixed in the sediments and/or in the plenum by biogeochemical processes. Anschutz et al (2007) have found that a portion of the phosphate and ammonium released during mineralization does not escape the carbonated sediment of a coastal lagoon (Thau, near the city of Marseille, France). However, since highly complex processes of adsorption and desorption controlled by magnesium, iron and other minerals drive the adsorption and desorption of DIC (Millero et al., 2001) the above-mentioned presumption is a working hypothesis rather than an explanation.

Conclusion

More than 150 years after the first successful attempts to keep naturally balanced marine microcosms we start to understand how they function. The present paper has raised hypotheses, which may explain how biogeochemical processes have achieved a quasi-perfect homeostasis in reef microcosm. However, several questions were disregarded and since the biogeochemistry of a microcosm is likely as complex as that the ocean we have to keep in mind that turning hypotheses into scientifically established facts will require a tremendous amount of work.

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