"Goethe's Final Words"

an essay by

John E. McCosker

9 November 1981

Goethe's final words on his death bed were "mehr licht, mehr licht". Light, more light. Goethe was a genius, not just a poet and writer but a scientist, philosopher,and biologist as well.

Faust, if you will recall, was blinded, but in the end he saw and achieved. If Faust is in fact an autobiographical statement of Goethe's view of achievement in life, I must presume that his last words, "Mehr licht", were a plea for enlightment.

In this essay, I hope to enlighten you in a field that is well-deserving of enlightment, and about which much has come to light within my own lifetime. I propose to take you on a sea voyage through the verdant meadows of her surface to her dark and monotonous abyssal benthos. We will stop at various levels along the way to investigate the adaptations that plants and animals have made with regard to the amount and kind of available light.

The oceans and seas have an average depth of four kilometers,

yet it is only the upper 200 meters or less of clear oceanic water that is illuminated with light of sufficient intensity and quality to allow photosynthesis. The light available in this illuminated layer, call the euphotic zone, is dependent upon the amount of solar radiation striking the sea's surface, the amount reflected back to the sky, and the absorptive materials within the water which reduce its transparency. Ultimately, all light energy is thus scattered, reflected, and absorbed. It is the absorption of light by living plants that supports life on our planet through photosynthesis, the solar assisted conversion of carbon dioxide and water to organic compounds and oxygen. Marine biologists measure the rate of this organic turnover, called primary production, and have learned enough within the last several decades to realize how much they still don't know.

In recent decades, oceanographers towed plankton nets behind their vessels to discover the large scale variations in the amounts and kinds of plankton at each locale. Now, with the aid of satellite surveillance, the chlorophyll content of seawater can be measured, transmitted, and translated to indicate phytoplankton abundance at a given location. This seasonal and latitudinal variation of plant life is significant to mankind because of the fisheries which rely directly (or through zooplankton and zooplanktivorous intermediaries) upon local phytoplankton. Seawater has physical properties vis à vis light transmission which nicely explain the adaptations that plants have made to life in the sea.

Seawater diffentially absorbs the component wavelengths of light. (Recall throughout this discussion that the color one observes is the particular spectrum reflected by the object; other wavelenghts have been absorbed.) The ozone layer, atmospheric particles, and cloud cover effectively filter out most of the ultraviolet light, resulting in a spectrum from near ultraviolet to infrared at the seasurface. Infrared, red, and dark blue ultraviolet wavelengths are absorbed within the first few meters of oceanic water, such that at ten meters depth light is predominantly blue-green in color. (This brings to mind the vintage Mike Nelson undersea films--they were always blue-green, except as seen on black and white television, because natural lighting unaided by underwater lamps was used.) This differential absorption is more apparent in coastal waters which are affected by sedimentation carried by runoff and high plankton populations, than in the more transparent oceanic waters which permit strong blue-green light passage to 100 meters or so.

Perhaps if we were fitted with seawater-simulated contact lenses, we might better appreciate what life is like in a world without red hues. Most shallow water fishes have a retina complete with cones for color viewing and rods for detailed black and white vision. As one might suspect, the optimal color reception of each species studied happens to coincide with the spectrum of light which penetrates to the depth the creature inhabits. A further curiosity arises when a fisherman, armed with this information, reels up his first Red Snapper, a vermillion trophy from a depth of 50 meters or so. If

red light does not penetrate to such a depth, and said Red Snapper can't see red, then "why is it red?" our fisherman might logically ask. The answer best proffered by a perplexed predator, is that a red fish at depth appears gray and fades into the miasmic murk of the nearshore reefs. Were the fish black it would be nicely silhouetted against the skylight of the reef face, and become a quicker meal for a midwater predator with a preponderance of high contrast rods in his retina.

In their evolution, marine plants have, like fishes, finely tuned their light gathering pigments to the spectra available to them. Their purpose is not vision or camouflage, but photosynthesis. Among the photosynthetic pigments of phytoplankton are carotenoids and chloroplasts which capture red and blue light and in turn reflect the green. The absorption peaks of the various attached and planktonic algae nicely coincide with the kind and intensity of available light.

The large attached algae of the sea, collectively known as kelp or seaweeds, is limited to the narrow coastal zone, living in 100 meters depth or less. As previously mentioned, the longer, red wavelengths do not penetrate below several meters, such that complimentary colors are absorbed and utilized by the plants. A colorful vertical zonation exists beginning with the green sea-lettuces and their relatives which live in the shallowest water, beneath which live the red and the brown algae. The reds are of

gustatory significance and, as nori, have been cultured and enjoyed by Oriental island societies. The giant kelps, brown algae of the coasts of California and Peru, are of greater economic significance because of their harvest and the extraction of algin from the plant. Algin is used as an emulsifier by the seaweed to give it the resilience necessary to withstand the surge and swell of the nearshore environment, and by mankind in such diverse products as cosmetics, pharmaceuticals, ice cream and beer. Giant kelp is harvested by equally giant sea-going lawnmowers, whose blades mow a continuous swath six meters across. Healthy kelp grows at a remarkable rate, and at more than a meter a day it is the world's fastest growing plant.

The oceans, thank goodness, are interconnected but not homogeneous. My concern is not for biologist's boredom, but rather because the vastness of the oceans would make them impossible to exploit efficiently except for the fact that primary porductivity can vary by two orders of magnitude between locations. The potential food value of the sea, ranging from the gourmet kazunoku sea urchin roe to krill-enriched flour, ultimately relies upon the phytoplankton. This sunlight is transferred in energy packets from consumer to consumer along food chains of various links and efficiencies. The efficiency of a food chain decreases with the increasing number of steps, just as one can envision an inverted pyramid of food energy funneling downward from the sun through pastures through

grazing cattle to man the ultimate consumer. It boggles my mind when I realize that a football field's equivalent of grass will ultimately become a hamburger. The oceanic food chain that man exploits usually has four or five steps, such as sun → photoplankton → zooplankton → krill or small fish → tuna-sized fish → fisherman. One may assume that eighty to ninety percent of the energy is lost to animal maintenance at each transfer, thus only 0.1 percent of the original solar energy ends up in the fish dinner which we consume.

Not coincidentally, the greatest vertebrates of the sea are eating lower down the food chain to save energy. The great whales (the largest vertebrates ever on this planet) and the greatest fishes (the whale shark, basking shark, and megamouth shark) eat krill or smaller plankton which in turn have fed on copepods or diatoms, and thus by their dietary preference are 10 to 100 times more efficient at harvesting the productivity of the sea than they would be as fish eaters.

The most productive fish-producing areas of the world are those where primary productivity is highest and the food chains are the shortest. These oceanic cornucopias are called the Upwelling Regions. This phenonmenon occurs primarily along the temperate and subtropical western continental margins (including California, Peru, northwest and southwest Africa, the Arabian coast, and Somalia), where, due to the rotation of the planet and its resultant gyral effect upon moving water (the Coriolis Effect), nurtient-rich deepwater replaces nurtient-poor surface water driven offshore by coastal winds. These upwelling zones

comprise but 0.1 percent of oceanic water, an area smaller than California, but are responsible for more than one-half of the entire world's fish catch.

This excessive dependence upon such a small portion of the sea for harvesting raises serious questions. Such as, what if the upwelling were to stop? It does, occasionally, during a nearly cyclical phenomenon called El Niño in Peru, in honor of the Christmas child. Its gift however is warm nutrient-poor surface water,and in 1972 it resulted in the collapse of the world's largest fishery. So the sun, in spite of its willingness and warmth, cannot prime the oceanographic productivity pump unless the necessary nutrients are there as well. But now, I return to the lowly alga.

My first foray with scuba tanks through a giant Macrocystis kelpbed reminded me of walks I had taken through Yosemite. The bright orange Garibaldi swimming through the kelp canopy formed an image not unlike that of a colorful Western Tanager flitting through a redwood grove. This giant brown alga forms the matrix of the community within which the seals, sea otters, fishes, invertebrates and other plants find food and refuge.

In the tropics the matrix is provided by the skeletons of myriads of once-living coelenterates, whose living polyps secreted the calcium carbonate substance that is a coral reef. In recent years, invertebrate zoologists have discovered that the coral polyp cannot perform this architectural triumph alone, but depends heavily upon symbiotic algae that live within their tissues. Sunlight is captured by the blue-green zooxanthellae live-ins, releasing oxygen through the photosynthetic reaction

which is consumed, along with an occasional meal of algae, by the growing coral. For that reason, coral growth is limited to brightly sunlit, transparent shallow seas, and to shallow depths as well. Coral growth and structure appears as if it were the creation of a sun-worshiping Palm Springs' designer. In lagoons and on leeward shores, where storm and swell cannot break their structure, corals grow in delicate fan-like shapes, maximizing the available light just as the leaves of trees in the forest maximally capture whatever sunlight filters down from the sky above. In more turbulent, wave-swept water, corals have sacrificed lacy breadth for strength, avoiding water resistance by being slender or dome shaped.

Usually the first reaction of a surfacing novice snorkler is "Why are coral reef fishes so colorful?" More precisely, how can they afford such gaudy bodies if, as we are told, a predator lurks behind each branching coral? No simple answer exists, but one must safely assume that it serves both a camouflage and communicative, or signal, purpose. The bizarre shapes and colorful pigment-laden polyps of corals provide fish with a confusing background such that a predator has difficulty zeroing in on its prey. Furthermore, the conspicuous and distracting patterns of shallow water fish, in an op-art fashion, disrupt the tell-tale outline that is important to the search image of a predator. Thus, camouflaged coloration is useful even to a blind invertebrate, but what is its communicative value if the viewer can't see color, or even differentiate hues? Apparently many can.

It seems inductively obvious that the gaudy livery sported by aforementioned coral reef butterflyfish and angelfish must serve

a purpose other than camouflage. The signal value of shocking red stripes advertizes the presence and attitude of the individual, and has inadvertently generated a colorful debate amongst Konrad Lorenz and a school of fish ethologists as to the value and significance of the "Poster Coloration" of coral reef fishes. The deductive evidence for color vision comes from many sources, including the microscopic anatomy of the retina, laboratory experimentation with living fishes, and the many freshwater fisherman who have learned that on certain days the the Quill Gordon is preferable to the Ginger Quill on a sunlit troutstream.

Most shallow water fish have a retina containing both rods and a variety of cone types. Deep sea fish, with few exceptions, have a pure rod retina; a variety of colors, you will recall, are unavailable at depth. Mid-depth fishes have shifted their spectral sensitivity to the short wavelengths, making them more sensitive to the blue wavelengths that best penetrate clear water. This shortwave shift has been made by all the vertebrates that live and swim in that limited color band, including the whales, seals, bony fishes and sharks. A few remarkable exceptions exist in the deep ocean, such as a certain black dragonfish which both emits and receives red light. Since most of its midwater compatriots are color-blind (they possess an all-rod retina), such a red-emitting predatory species would in effect possess a "sniperscope" that its prey are color-blind to and oblivious of.

Without the protection of a reef or the darkness of depth, what is a helpless sardine to do for protection in open water?

The survivors are those that natural selection has favored with schooling behavior and adaptive, two-tone coloration. Sunlight penetration in clear nearshore and oceanic waters has necessitated a camouflaged livery to protect such potential prey items and also, to disguise an approaching predator. Nearly all motile open water animals are "countershaded" such that they are generally darker on their dorsal surface, lighter along their ventral surface, and silvery in side view. Such a coloration renders an animal nearly invisible from any angle. Thus a silver-sided, blue-backed sardine is nearly invisible when seen from above by a diving pelican which sees only blue below, as well as to the equally contershaded tuna beneath it which looks hungrily up to the surface and sees only the bouncing light penetrating through the sea surface.

Animals in deeper water, at 500 meters depth for example, are illuminated enough by downwelling light that they appear silhouetted against the overlying water column. This phenomenon was inferentially deduced by ichthyologists more than a century ago, many decades prior to man's first descent in a deep-diving submersible. Early anatomists recognized the large up-turned and telescoping eyes of midwater-trawled fishes. Consider the bizarre Barrel-Eye, a midwater, fist-sized fish which lives in depths of 200-600 meters, looking forever upward for the silhouette of a slowly passing prey, potential predator, or another Barrel-Eye of the opposite sex who's willing as well. Its hunt is complicated by the counterevolutionary gambit of potential prey species which countershade ("counterlight", actually) themselves with a series of dimly-glowing luminescent organs,

serially arranged along their ventral surface from chin to tail fin, producing a weak blue-green glow that is equal in intensity to the downwelling sunlight. Freshly captured lanternfishes and mesopelagic squids and shrimp have been place in experimental chambers which precisely simulate the light of the mesopelagic zone. As the experimenter increases the overhead lights, the fish, shrimp, or squid increases its ventral lighting in unison, providing an experimental verification of what probably occurs when a moonlit sky becomes darkened by cloud cover or the individual raises or lowers itself within the water column. The light receptors which control a fish or shrimp's own rheostat were identified in a series of inventive experiments wherein a set of miniature eye shields or sunglasses were fitted for the animals, demonstrating that the compound eye of the shrimp and the supraorbital photophore of the lanternfish are the measuring devices of the feedback systems.

The deeper midwater zones called the mesopelagic (arbitrarily defined as 200-1000 meters) and bathypelagic (below 1000 meters) contain some of the most bizarre and curious of known living creatures. The upper mesopelagic fishes encounter some light, and are countershaded and/or counterlighted as mentioned above. The enlarged eye of fishes such as the Platyberyx or the Hatchetfish is an attempt to gather as much of the available light as possible. In the absence of photosysthesis, available meals are limited to what rains down from above or the fellow sitting at the dinner table with you; such conditions have resulted in toothy maws like that of the Fangtooth, adapted to

enjoy a large and struggling, but infrequent meal, or the Umbrellamouth Gulper Eel, which feeds on enormous prey that are swallowed into an incredibly distendable throat and stomach.

In descending from the surface to the meso- and bathypelagic layers, both life and light dramatically disappear with increasing depth. Surface biomass is reduced to approximately one-fifth by the upper mesopelagic, then falls another quantum to one-fiftieth of the overlying biomass in the lightless abyssal zone. The abyssal plains lie below the continental slope and span nearly half of the Earth's surface. This is thus the largest, single habitat on Earth, a relatively stable habitat with a very predictable range of environmental parameters.

An interesting comparison can be made by suggesting that the deep sea is "like a desert", evidenced by the paucity of living material. This comparison, although valid, is ironic in that the sunbathed deserts are lacking in moisture, whereas the aquatic realm of the Abyss is awash in water but limited by the lack of food-providing sunlight.

Abyssal dwellers have made adaptations to live entirely without light. As a species that depends on vision as the primary sensory modality, it is difficult for man to appreciate the increased sensitivity and use made of the other environmental receptors available to and used by blind creatures. Abyssal animals have little knowledge of or care for the season of the year of the time of the day. The uniformity and constancy of temperature, darkness, and minimal food availability have given creatures an environment they can count on and adapt to.

Sunlight never reached those frigid plains to illuminate the slow moving creatures of the Abyss until three decades ago when the lights of pressure-protected submersible camera equipment punctuated the Abyssal monotony with an occasional stroboscopic blast. Oceanographers and marine biologists are now piecing together a patchwork amalgam of data collected by deep sea trawl nets and dredges and, more recently, the photographs taken from deep-sea robot cameras and submersibles. What they are learning about the largest, single habitat on Earth is not coming easily, for the sampling problems of studying the Abyss are as enormous as the pressures encountered therein.

Marine scientist Sylvia Earle graphically portrayed the knowledge of the Abyss when she reminded me that "Man's footprints were left on the surface of the moon, yet none mark the average floor of the Sea." Dr. Earle placed the sampling and analysis problems in proper perspective when she testified before the April, 1979, Senate Hearings on Deep-Sea Mining. She asked the senators to "Imagine, if you will, that you're flying over a fogbound forest in a slow-moving blimp. You can't see the ground,but an instrument tells you that it's about 1,000 meters below you. You don't know exactly where you are, so your chances of returning to the same location are slim. To get some idea of what the forest below is like, you drop a line with a bucket attached, then tow the basket behind you and hope it will not get snagged or broken. After a while, you pull it up; you're thankful for anything that has

been snared--a rock, a twig, or perhaps a bewildered mouse."

The difficulties described by Dr. Earle were precisely those encountered by the seminal ocenaographic expedition whose purpose was to chart the chemistry, the topography, and the life of the deep-sea. This was the Challenger Expedition of 1872-1876. Nearly a century earlier, Pierre Simon, the Marquis de Laplace, calculated the average depth of the Atlantic Ocean. His method of calculation is as remarkable as the astonishing effect that his discovery made upon the scientific community. (His accurate prediction that the Atlantic seabed was 4,000 meters deep, was base upon his recalculation of the Newtonian explanation of the tidal interaction of the sun, Earth, and moon as it relates to wave passage and velocity between Brazil and the African Coast.) The implication of Laplace's discovery suggested to 18th century European scientists that life could not exist at such depths, where the pressures of 440 atmospheres (approximately 3 tons/square inch) and the absence of light would preclude life as they understood it.

Two Norwegian naturalists discovered that life <u>did exist</u> at greater depths when in 1864 they collected a stalked crinoid from 1700 fathoms (3109 meters). Its scientific description and related events resulted in a series of English expeditions named for the vessels which bore them, such as <u>Bulldog</u>, <u>Lightning</u>, <u>Porcupine</u>, <u>Valarous,</u> <u>Shearwater</u>, and the most important, the <u>Challenger</u>. The Challenger Reports spanned 50 volumes and included the descriptions of 715 new genera and 4,417 new species of marine organisms, telling evidence not only of life but also of its diversity in the deep sea.

Although difficult to sample, the deep-sea is a relatively stable environment with a narrow range of parameters. The Abyss is aphotic (lightless) except for the chemical light produced by bioluminescent creatures. In that all of the wavelengths of natural light are absorbed in the euphotic zone, creatures of the Abyss tend to bear a uniform and somber livery of gray or black. The absence of light precludes the existence of living photosynthetic plants, that is organic primary production. Energy, therefore, is very limited in the Abyss. The physical and chemical characteristics of the Abyss are relatively constant. Seasonal changes, even days and nights, are imperceptible. Temperature extremes of the worldwide Abyss range from -0.6° to +3.6°C and within a certain locale it is nearly invariable. The salinity of Abyssal water is relatively constant at about 33 to 35 parts per thousand. Oxygen, although as low as three parts per million, is abundant enough to support the sparse life that exists. The Abyssal benthic bottom is covered with the oozing remains of fallen planktonic organisms mixed with mud. Such calcareous oozes are composed of myriads of microscopic foramenifera and coccolithophores to a depth of 4,000 meters. Below that depth, calcium carbonate structures begin to dissolve with the increasing pressure and are replaced by red clay and an abundance of aluminum, iron, copper and manganese. The commercial value of the manganese nodules which festoon her benthic bottom has brought international attention to the future of deep-sea mining. Conservative estimates of 1,500,000,000 tons of manganese nodules exist for the Abyssal

plain west of Pacific Mexico. (The antiquity of that mineral wealth is considerable if hypothesized accretion rates of .001 mm/century are correct.) The general topography is uniform across wide expanses of the Abyssal Plains, punctuated over millions of kilometers by an Abyssal hill, hummock, rise or seamount.

Energy, in the form of food, is apparently the limiting factor for Abyssal life. Organisms which inhabit the Abyss are primarily sediment-feeding, at (epifaunal) or near-surface (infaunal) mud-dwellers. Epifaunal invertebrates have evolved or accentuated appendages which root them to the surface layer, such as the stalked crinoids or glass sponges, or perch them delicately above it like the brittle stars and sea urchins. Energy, thus, rains down from above in the form of detritus, dead algae and macroanimals which sink from the overlying surface waters.

It is presumed that the Abyss has been populated by shallow water forms that have invaded the deep-sea and adapted to the lightless, low energy, nearly uniform topography of the environment. Most organisms are small, extremely slow moving and slow growing, and require a considerably longer time-span to reach sexual maturity than their shallow water relatives. Karl Turekian of Yale University, for example, used radium-228 dating procedures to verify that a small bivalve clam reached sexual maturity at 50 years. Bivalves of the Abyssal Plain of the North Atlantic are thought to live 250 years or more, yet only attain a length of a centimeter or so. As well as slow growth rates, deep-sea

animals typically have smaller brood-sizes and population age structures which are not dominated by younger age classes, features which differ significantly from the life history phenomena typical of animals inhabiting a coral reef or a tropical rain forest. Those differences from the Abyssal condition are explained by biologists to be a result of the predation-controlled, more variable environments that their more shoaler cousins experience.

After solving the problems of eat or be eaten within the deep-sea environment, the necessity of reproduction remains. Low populations sizes and reduced individual activity reduce the chance of a meeting between consenting adults. Abyssal fishes have accomodated themselves to this nearly uniform and nearly seasonless world in a number of ways. Imagine the problems of mate location in a lightless world--should a species in a romantic mood be desirous of a mate, what is the chance that the fish it encounters will be of the right species, the right sex and again, I submit, willing as well? To overcome these difficulties, many species in this aphotic zone have greatly enlarged their olfactory apparatus so that they can discover a mate by current-carried odor cues. Others, such as the Grenadiers and Brotulids, produce sound to attract a mate. Others have increased their search odds and become functional hermaphrodites(and in some cases, self-fertilizing hermaphrodites), insuring fertilization at the cost of a reduction in genetic variability. Certain of the ceratioid angler fishes have reached the ultimate in mate insurance, wherein the male of those species becomes a small appendage of

the female, attaching his body to hers in a "parasitic" fusion, gaining continual sustenance in exchange for his sperm.

It is most unfortunate that Goethe and his contemporaries did not live long enough to see what scientists saw in 1977 through the porthole of Alvin, a research submersible. This most remarkable discovery, made while diving along submarine ridges southeast of the Galapagos Islands, evidenced an entirely different biological approach to life. Bacteria living along the edge of the hydrothermal vents of the Galapagos Rift Zone, a submarine volcanic fissure more than 2500 meters below the surface, have evolved to become "chemoautotrophic", nourishing themselves not on the energy from sunlight trapped by plants but on the synthesis of hydrogen sulfide from the chemical soup they are living in. These bacteria are the basis of a food chain that includes fishes, crabs, clams,and strange coelenterates called "dandelions".

For me, the excitment of the Galapagos' discovery is not what was found, but that we are still able to make such a finding. Such a discovery should be a signal to the next generation of oceanographers that much remains to be seen.

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