Marine biodiversity characteristics

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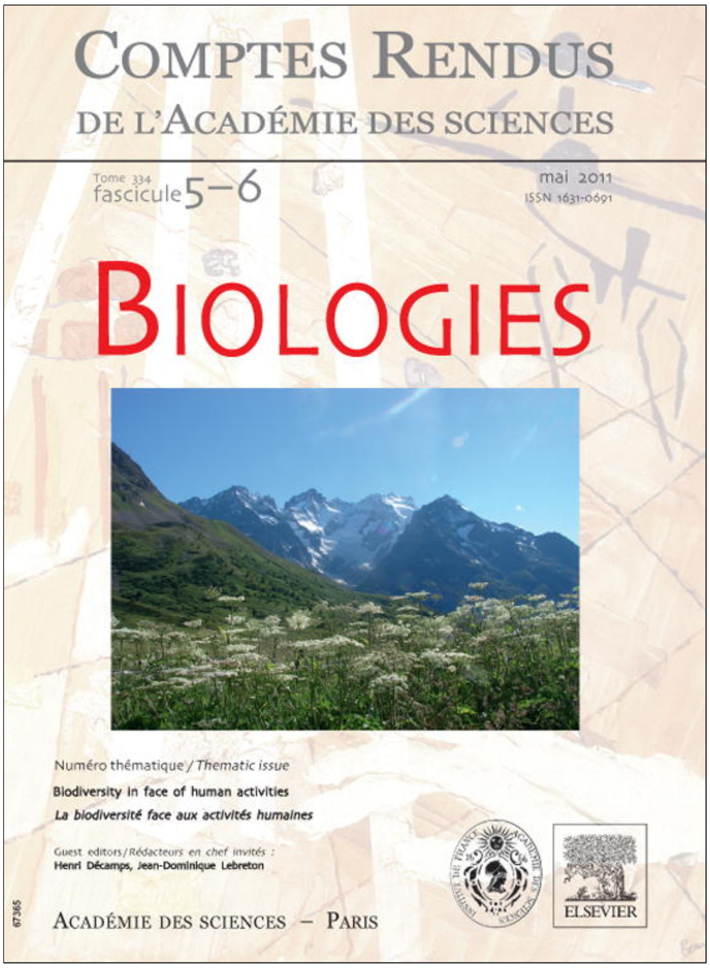
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Les spécificités de la biodiversité marine

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A B S T R A C T

Oceans contain the largest living volume of the "blue" planet, inhabited by approximately 235–250,000 described species, all groups included. They only represent some 13% of the known species on the Earth, but the marine biomasses are really huge. Marine phytoplankton alone represents half the production of organic matter on Earth while marine bacteria represent more than 10%. Life first appeared in the oceans more than 3.8 billion years ago and several determining events took place that changed the course of life, ranging from the development of the cell nucleus to sexual reproduction going through multi-cellular organisms and the capture of organelles. Of the 31 animal phyla currently listed, 12 are exclusively marine phyla and have never left the ocean. An interesting question is to try to understand why there are so few marine species versus land species? This pattern of distribution seems pretty recent in the course of Evolution. From an exclusively marine world, since the beginning until 440 million years ago, land number of species much increased 110 million years ago. Specific diversity and ancestral roles, in addition to organizational models and original behaviors, have made marine organisms excellent reservoirs for identifying and extracting molecules ($>$ 15,000 today) with pharmacological potential. They also make particularly relevant models for both fundamental and applied research. Some marine models have been the source of essential discoveries in life sciences. From this diversity, the ocean provides humankind with renewable resources, which are highly threatened today and need more adequate management to preserve ocean habitats, stocks and biodiversity.

Mots clés :
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Modèles marins

R É S U M É

Les océans constituent le plus grand volume offert au vivant sur la planète « bleue » et abritent aujourd'hui entre 235 et 250 000 espèces décrites, tous groupes confondus. Celles-ci représentent quelques 13 % des espèces connues actuellement sur le globe mais les biomasses marines peuvent être considérables, le seul phytoplancton représentant plus de la moitié de la biomasse de la planète, les bactéries marines plus de 10 %. La Vie est apparue dans l'océan ancestral il y a plus de 3,8 milliards d'années et y a subi plusieurs événements déterminants, de l'apparition du noyau de la cellule au développement de la sexualité, en passant par la « *multi-cellularité* » et la capture des organites. Sur les 31 grands *phyla* animaux actuels, 12 sont exclusivement marins et n'ont jamais quitté l'océan. Une intéressante question a trait à la comparaison du nombre d'espèces en mer et sur terre. La

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différence observée actuelle semble être apparue récemment dans l'évolution. La vie a tout d'abord été exclusivement marine jusque vers 440 millions d'années (pour la vie « métazoaire élaborée ») puis a explosé en nombre d'espèces sur les continents vers 110 millions d'années. Cette diversité spécifique et l'ancestralité des caractères, ainsi que des schémas d'organisations et de comportements originaux, font des organismes marins d'excellents réservoirs de molécules d'intérêt pharmacologique (plus de 15 000 aujourd'hui identifiées et extraites) et/ou de modèles d'étude particulièrement pertinents en recherche tant fondamentale que finalisée. Certains modèles marins ont été à la base de découvertes essentielles en Sciences du vivant. La biodiversité océanique fournit à l'humanité des ressources renouvelables, bien menacées aujourd'hui, qu'elle doit absolument mieux gérer en préservant les écosystèmes, les stocks et la biodiversité.

1. Introduction

Oceans constitute the largest volume of life on the planet (1.37 billion cubic kilometers) covering 70.8% of the Earth's surface, or 361 million square km. The average ocean depth is approximately 3700 m and the main feature of this gigantic community is its connectivity. Another special feature of the ocean is its salinity, compared to all the rest of free-standing water on the planet. In the open seas, salinity is extremely stable at 35 psu[1] and the composition of oceanic water is the same everywhere, as is has been for several hundred million years (components, osmolarity, pH).

The species diversity found in oceans does not exceed 13% of all the living species currently described, i.e. approximately between 235 and 250,000 species, all groups included [1]. This is low and may be due to two reasons. Firstly, our knowledge of ocean life – particularly with regard to the ocean depths and microorganisms, bacteria and especially microalgae – is probably more incomplete than on continents: we therefore underestimate overall ocean biodiversity. New approaches, such as combining flow cytometry and molecular probes used to detect microorganisms with high specificity, have uncovered an extraordinary and completely unanticipated degree of biological diversity. "Ocean sequencing", which is the sequencing of all DNA in a volume of filtered ocean water, points to the same conclusion, as the data obtained lead to the discovery of a tremendous amount of new species (about 80%). For all prokaryotes and very small eukaryotes, recently developed molecular approaches (ribosomal RNA sequencing, including 16S and 18S) are constantly providing an astonishing array of knowledge [2]. Secondly, marine biotopes with their continuous environment (total connectivity) and the species that inhabit them – through gamete and larval stage dispersion – are clearly less predisposed to strict endemism than terrestrial biotopes where many boundaries and isolates can favor speciation more easily, leading to significant differences in specific diversity. In addition, marine ecological niches are less varied than terrestrial ecological niches, and do not offer a similar compartmentalization for the development of new species, although they are characterized by huge biomasses.

[1] psu: practical salinity units (international unit), corresponding to 35 g of NaCl per litre of solution.

2. The story of diversity

The age of the Earth has been estimated at 4.6 billion years (By). Life appeared in the ocean relatively rapidly after the initial cooling and condensation of water masses, approximately 3.9 By ago. On Earth, water exists under solid, vapor and liquid forms. The most ancient sedimentary rocks known to man (on Akilia Island, in southern Greenland) contain organic carbon dating back to 3.85 By. According to some authors [3], the Planet Earth was in such an ideal position with regard to the Sun that the emergence of life was inevitable. Primitive life must be conceived of as having been very simple at the start, emerging from a world of RNA and proto-cellular structures [4]. The current deposits of stromatolites are very precious because their carbonated segments contain the oldest fossils of microorganisms, cyanobacteria. They belong to the first ocean colonies of life that emerged between approximately 3.4 and 3.2 By, when there was no oxygen in the atmosphere. With the presence of specific cell pigments, photosynthesis was developed in a water environment, producing oxygen and sugars from light and carbon dioxide (CO_2). This process appeared on Earth around 3.5 By. Then, oxygen began to diffuse outside of the aquatic environment around 3.2–2.7 By ago. The current composition of the atmosphere with a 21% oxygen content dates back approximately 100 million years (My), during the Cretaceous period.

Some events determined the outcome for life and biodiversity in these ancient seas: the development of the nuclear membranes and the individual nucleus (transition from prokaryote to eukaryote status) around 2.2 By; the emergence of multi-cellular organisms and metazoans around 2.1 By [5]; the capture of surrounding cyanobacteria that would become symbionts and cell organelles such as mitochondria and plastids, with their own small DNA, around 1.9 and 1.4 By, respectively. The emergence of sexual reproduction occurred in the ancestral sea about 1.5 By ago – an extremely important event for the development of biodiversity – at the origin of unprecedented novelty and diversity at a much more rapid rate. For example, sexuality prevalence accelerated the arm races between parasites and their hosts through co-evolution and molecular dialogue [6], with new genes and sexual selection able to act.

Organized metazoan life emerged from the ocean after the explosion of the end of Pre-Cambrian life which occurred 570 My ago. The first plant life (first vascular plants in the Upper Silurian, approximately 440 My ago) and land animals including arthropods and Chordates would leave their mark on the continents approximately 440-430 My ago largely before the base of the Devonian Period: Myriapods, Scorpions, Dipnoi (lungfish), *Rhipidistia*, *Ichthyostega* (one Amphibian)... Numerous new adaptations were developed in plants as well as in animals, as the shift to terrestrial life and air breathing was an exceptional development in the history of Life. The differences between aquatic and terrestrial animals are fundamental ones. In the first group, small species draw oxygen from the water by diffusion toward their deepest parts, while larger species (or stages) have developed gills. Seawater contains approximately 30 times less oxygen than air. Anisosmotic aquatic organisms (species maintaining in a narrow range their internal osmolarity, not depending on the salinity of the ambient water) cannot develop a very large surface area for exchange (gills) because of the inherent dangers of physical osmotic flow (water and electrolytes): the animal is in danger of losing its water in the salty ocean, or being "drowned" in freshwater. In fact, fish are constantly subjected to a delicate compromise between developing a maximum surface area for oxygen capture in a poorly oxygenated and changeable environment, or a minimum surface area to avoid a severe loss or gain of water and mineral equilibrium [7]. Terrestrial animals on the other hand are faced with UV rays (also affecting aquatic species in shallow waters), dehydration, different weight-bearing requirements (requiring a heavier and more resistant skeleton and a consequently heavier muscle mass) and have to develop a different type of excreta with little or no toxicity (uric acid, urea). Aquatic animals secrete ammonia and the vast majority cannot regulate their body heat. Much later, during the Triassic Period, approximately 210 My ago and following the third great extinction crisis (245 My), the first models of thermoregulation emerged and were optimally efficient in large dinosaurs, and then, particularly in Birds and Mammals.

A very good example of the plasticity of the living and return to the ocean is illustrated by the Cetaceans, which started this "re-acclimatization" around 50–55 MY ago from basal *Diacodexis*-related Artiodactyls that were first essentially terrestrial (*Pakicetus*) and then amphibious (such as *Ambulocetus* or *Rodhocetus*). The recent gigantic cetaceans, which are among the largest animals that ever inhabited the planet since the origins of Life (and which humans have cheerfully hunted down and killed for the last hundred years!) are very recent in origin (Plio-Pleistocene, i.e. the blue whale, about 2 MY). Today, 12 animal phyla are exclusively marine and have never left the ocean (Echinoderms, Brachiopods, *Chaetognatha*, etc.) (Table 1). There are only two groups (and no complete *phyla*) that are exclusively "continental": Myriapods and Amphibians (the last ones living in both freshwater and in the air). The ocean biomass is considerable as well: the bacteria from the sub-surface of the ocean alone represent more than 10% of the entire carbon-based biomass on the planet [8], and the marine phytoplankton more than half of it [9].

Marine environment has therefore played a determinant role in the history of Life, and the current ocean preserves its primordial role in biological and climate evolution, biological because the age of marine Life and still the presence of ancient groups, climatic because it represents a huge aquatic environment, very active on Planet climate control.

Every living being is made of water, from a low water content in the "driest" organisms, such as plant seeds, up to 98% for some aquatic species such as algae, jellyfish, and ascidians. Water has been a truly determining factor in the History of Life, and scientists searching for traces of "extraterrestrial" life focus their efforts on water as the first key molecule of life, in addition to DNA, amino acids, ATP... [7]. The ocean is salty, primarily sodium chloride, and has been so for a very long time. Today we understand

Table 1
Animal phyla exclusively marine.

Phylum	Genus or species	Pelagic	Benthic
Placozoa	*Trichoplax adhaerens*, very small and flat animals, basal form of invertebrates, 3 sp		X
Ctenophora	From 1 mm to 1.5 m, *Pleurobrachia*, *Beroida*, *Cestum*, *Velamen*... Burgess shale, 190 sp	X	
Xenoturbellida	2 known species, *Xenoturlla westbladi*, small marine "worms" discovered in Scandinavia		X
Cycliophora	Microscopic animals transported on cold water lobsters, g. *Symbion*, 2 species		
Mesozoa	165 sp, small parasites of marine invertebrates, *Rhombozoa* and *Orthonectida*,		
Sipuncula	Sipunculid worms, *Sipunculus vulgaris*, since the Cambrian, non-segmented, 1284 sp,		X
Echiurians	*Metabonellia*, *Bonellia*, *Prometor*... marine "worms", 234 sp		X
Phoronidians	*Phoronis*, *Phoronopsis*... living in a cylindrical tube, 31 sp,		X
Brachiopoda	With a lophophore, a crown of tentacles, and shells, 12 000 fossils known, 441 sp today,		X
Echinodermata	Starfish, sea urchin, crinoids, sea cucumbers... > 14 000 sp,	X	X
Chaetognatha	"Arrow worms", 120 species in 20 genus, g *Spadella*, 280 sp,	X	X
Hemichordata	Worm-shaped marine deuterostomes, fossil Graptolites, *Saccoglossus*, 143 sp,		X
Cephalochordata *sub-phylum*	The amphioxus, lancelets, *Branchiostoma lanceolatum*, g *Assymetron*, 25 species		X
Tunicata *sub-phylum*	Urochordata, Ascidians, 3 000 sp in 4 classes, *Styela*, *Didemnum*, *Salpida*, *Appendicularia*...		X

Table 1 is just informative on the differences "marine life" versus "land life": classification is changing, i.e., Cephalochordata and Tunicata are *subphyla* of Chordata (of which, of course, there are land species!); Kinorhynca, Priapulida and Loricifera have been gathered in Cephalorhyncha (with land Nematomorpha); Xenoturbellida, Cycliophora and Mesozoa can be considered as valid phyla...

that this salinity is very stable: billions tons of cations (calcium, potassium, magnesium, sodium) have always flowed into the oceans from rivers and estuaries. Calcium is compensated for by uptake in marine sediments and the formation of limestone; Potassium is compensated for by adsorption in clay deposits. Magnesium and sodium are taken up by oceanic ridges (serpentine formation and clay enrichment of pyroxene and olivine). Bicarbonates are constantly being exchanged in the atmosphere and biosphere, and as for chlorides, which are not taken up by any large biogeochemistry cycle. It is now believed that chlorine was one of the original volatile elements that dissolved into the first seawaters and remained there (no fluvial contributions take place today). The current salinity of approximately 35 psu, develops an osmolarity (''osmotic pressure'') of 1050 mOsm.l^{-1}. Marine life has always had to depend on this osmolarity and developed, from bacteria to arthropods, a strategy of intracellular isosmotic regulation, in which the vast majority of invertebrates and some vertebrates have the same osmolarity (inner environment and cells) as ambient seawater. During a very long time, the major barrier to leave the marine environment was this salinity. Another strategy, which first appeared in certain crustaceans, is called extracellular anisosmotic regulation (see before): it enables a strong diadromous migration capacity (and adaptation potential to new environments of different salinities), by maintaining an osmolarity in cells and bodily fluids within strict limits (between 280 and 360 mOsm.l^{-1}; humans are at 302), in any degree of exterior salinity [7]. In fact, with this strategy, death from dehydration is possible in seawater, with the salty environment causing water to flow from the organism toward the exterior through surfaces of exchange in intimate contact with salt water (blood-water), epithelia inside the mouth and gills, salts from seawater migrating in the opposite direction. Marine osmoregulators (such as bony fish) have had to adopt strategies to constantly drink sea water while excreting salts via the gills, with the kidney undertaking the role of water conservation [7]. One of the main problems of land-based life is also water conservation and the struggle to avoid dehydration. The role of the kidney is therefore essential: a good example is the small kangaroo rat of the desert, which never has available water to drink and which secretes urine that is 9 times ''saltier'' than sea water! ''Terrestrial'' biodiversity exploded the first time during the Carboniferous Period starting 345 My ago and more recently, 110 MY ago.

3. Why so many differences between land and sea?

As mentioned above, today life on land is as much as six to seven times as diverse (species) as life in the sea. In comparison with marine species diversity, this extraordinarily high level has been achieved in a shorter time and occupies a much smaller area of the Earth's surface. Raw paleontological data suggest very different models for the diversification of life on land and in the sea [10]. The well-studied marine fossil record appears to show evidence for an equilibrium model of diversification, with phases of rapid radiation, followed by apparently quiet periods for new original organism diversification. The continental fossil record shows an exponential diversification from the Silurian to the present. These differences appear to be real: the continental fossil record is unlikely to be so poor that all evidence for a high initial equivalent diversity between sea and land has been lost. However, the apparently equilibrated marine model may be partly an artifact of the focus on the family level. At the species level, the rate of diversification may well have been exponential [10]. Nevertheless, the rocketing diversification rates of flowering plants, insects, and other terrestrial life are evidently hugely different from the more sluggish rates of diversification of life in the sea, perhaps as a result of greater endemism and habitat complexity on land. 110 My ago, terrestrial plants went through a burst of speciation. So did the pollinators, Fungi, herbivores and carnivores associated with them. These relationships made ''rare'' species possible, as plants acquired help in dispersing their pollen and seeds, resulting in relatively low population densities for individual species [11]. Quickly, on continental surfaces, their numbers left marine biodiversity way behind. Does it would mean that marine species would live a much longer time than land ones? Rare species in the sea are much less frequent, but we would need further careful checks of marine caves and hydrothermal vents. The possible trigger for the terrestrial explosion would be the evolution of a more efficient way in which terrestrial plants use water [12]: we go back to water topic!

Altogether, the level of endemism is much higher on land compared to the sea. The smallest endemic areas in the sea are of a few 10 km^2 while on land some are a few 100 m^2! This could be due to the physics of dissemination inside the sea, according to water density and viscosity and local water current regime. The land-sea disparity occurs even in diversity hot spots. A single hectare in a tropical rainforest may contain some 475 tree species and more than 25–50,000 insects. But a hectare of coral reef, often called the sea's ''rainforest,'' might be home to at most 300 coral, 600 fish, and about 200 algal species [11]. Furthermore, many stationary plants rely on animals to do the work of finding mates, transferring pollen, and spreading seeds. The strategy works well: today, more than 250,000 animal species are pollinators. In such a system, mobile pollinators and dispersers can maintain populations of rare individuals. With few exceptions, animal-mediated transfer of gametes, fertilized eggs or larvae, or seeds occurs only on land. Instead, marine organisms tend to live in higher-density communities and sometimes employ extraordinary measures for fertilization. Consider barnacles, which have penises that are 10 times the diameter of the body in order to reach a potential mate [11]! Nevertheless, marine organisms exhibit a wide range of reproductive and developmental modes through which sexual, sibling and parent–offspring conflicts can manifest. Moreover, the existence of multiple mating in these species increases the likelihood, as well as the degree, of these conflicts [13]. Because of the water's carrying capacity, eggs and larvae are transported easily and over long distances. Most marine species reproduce by external fertilization. However, some species fertilize internally, i.e. sharks and rays. Fish produce very large numbers of eggs and they also represent an important source of food in the food chain, from invisible phytoplankton to bite-sized parcels. In fact, fish eggs finally represent more food (99.999%) rather than juveniles (0.001%) [14]. Larval dispersion is easy because of the sea's physical environment. By contrast the most common terrestrial reproductive strategy places adult and juvenile life stages in close proximity. To increase the chance of sperm fertilizing eggs, many marine organisms (corals, barnacles, limpets, etc.) synchronize their spawning. In this manner their juveniles swamp all other planktonic predators, becoming the main zooplankton for long enough to become successful. Because of the many vagaries of their juvenile planktonic stages, recruitment is highly variable from one year to another [14].

The development of dispersed communities "is the key to the current extraordinary diversity of species on land" [12]: high-density populations are at increased risk of being eaten or wiped out by disease, while dispersed communities face reduced competition and predation. But flowering plants that evolved later sometimes squeezed in three to 10 times as many veins per millimeter. Those extra veins are correlated with increased photosynthetic capacity. Because tropical biodiversity is closely tied to precipitation and rainforest area, angiosperm climate modification may have promoted diversification of the angiosperms themselves, as well as radiations of diverse vertebrate and invertebrate animal lineages and of epiphytic plants. Their exceptional potential for environmental modification may have contributed to divergent responses to similar climates and global perturbations, like mass extinctions, before and after angiosperm evolutionary burst [15]. All this added energy set in motion a positive feedback loop that encouraged more specialization. Speciation is largely linked to external changes and new pressures of selection and these new organizations in a changing world allowed the emergence of a plenty of new species, mainly in the inter-tropical area. We have also to take into consideration that, presently, insects represent the two thirds of the specific diversity and that they are not marine. Only a few insect species live in the oceanic environment. On the other hand, can we consider that some 600,000 beetles represent "more biodiversity" than 300,000 plants? Biodiversity is much more than the only specific diversity [16]! Today, after billions and millions years of the massive influence of "natural" (but let's take care not to consider the human "out of Nature", we are inside and cannot survive without it!) ecological factors, osmotic pressure of the ocean, pH, temperature of both air and water, day-length, oxygen availability, atmospheric composition, etc., the most active engine on evolution is the human [17,18], the greatest evolutionary force!

4. Conclusion

Connectivity and limited changes create stability in the ocean. Oceans have very stable and often ancestral populations and communities, for pelagic and mainly deep benthic life. In depth and caves, species are protected against "aggressions" (radiations, rapid temperature changes, meteorite impacts...). All seas are interconnected, and in theory, all organisms could migrate to every other place in the sea. Marine environments are more homogenous and stable, and are less patchy. Seawater transportation of cells or organisms (plankton, gametes, larvae...) is very different, compared with the air [14]. Many marine habitats depend on adjacent areas for food and larvae and stationary organisms can survive catching food that passes by. All these facts in addition to the specific physicochemical seawater environment (density, viscosity, salinity, pH, etc.) create a very original system. The only marine phytoplankton accounts for half the production of organic matter on Earth and has declined during the past Century, questioning the future of marine ecosystems, geochemical cycling, ocean circulation and fisheries [9].

There is in fact only "one ocean" and a very large "diversity of lands". Life emerged in the ancestral ocean, and the present time ocean shelters a lot of ancient *phyla*, not many species but many *phyla* and a huge biomass. Specific diversity, associated to very original anatomical and biochemical organizations and behaviours have made marine organisms excellent reservoirs for identifying and extracting molecules with potential pharmacological or cosmetic use (currently over 15,000) and/or to build especially relevant models for both fundamental and applied research [2,19]. Some marine models have been the source of essential discoveries in life sciences and Nobel Prize winning research in Chemistry and Physiology and Medicine[2] [2]. Ocean ecosystems provide humankind with renewable resources, which are highly threatened today, and deserve more adequate management in order to preserve stocks and biodiversity. Destruction and pollution of coastal areas, overexploitation (fisheries), dissemination of alien invasive species impoverish marine biodiversity, in addition to climatic change, including temperature increase, global acidification, sometimes de-oxygenation and sea level rise [1,16,20–23].

At the World Conference of Johannesburg in 2002, it had been suggested to slow (or even stop!) the erosion of biodiversity for 2010. Recent studies [21] clearly demonstrate that we failed in such an aim–never the erosion of biodiversity has been so high and a lot of marine ecosystems are particularly threatened [16,23–26]. Therefore, the UNESCO Conference in Paris, January 2010, proposed to move the date of the Johannesburg resolution from 2010 to 2020. Will we be able to better succeed for a target we were not able to reach between 2002 and 2010?

[2] Three examples among others: Elie Metchnikoff (Nobel laureate en 1908) used starfish larvae to observe the universal mechanism he would call phagocytosis, setting the foundations for non-specific immune defence and highlighting the importance of this mechanism as the oldest immune strategy. He opened the way for research in cell and comparative immunology that would set the stage for understanding reactions to infection and infectious diseases in humans. From the sea urchin ovocytes, T Hunt (Nobel laureate in 2001) identified an essential protein controlling the regulation of the cell cycle – cyclin B. Associated with kinase Cdc2, discovered in the yeast, it forms a dimer that makes up the well-known MPF (Meiosis Promoting Factor, now called the M-phase promoting factor). Purification of this universal factor from starfish ovocytes provided proof of the composition of the heterodimer, key-molecule in cancer development. A Hodgkin and A Huxley (Nobel laureates in 1963) carried out experiments on the transmission of nervous impulses, using a squid axon, with a cross-section that is 1000 times larger than mammalian axons, and showed the movements of ions from one side to the other of the neural plasma membrane [2].

Disclosure of interest

The author declare that he has no conflicts of interest concerning this article.

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