

A physiological approach to oceanic processes and glacial-interglacial changes in atmospheric CO₂

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SUMMARY: One possible path for exploring the Earth's far-from-equilibrium homeostasis is to assume that it results from the organisation of optimal pulsating systems, analogous to that in complex living beings. Under this premise it becomes natural to examine the Earth's organisation using physiological-like variables. Here we identify some of these main variables for the ocean's circulatory system: pump rate, stroke volume, carbon and nutrient arterial-venous differences, inorganic nutrients and carbon supply, and metabolic rate. The stroke volume is proportional to the water transported into the thermocline and deep oceans, and the arterial-venous differences occur between recently-upwelled deep waters and very productive high-latitudes waters, with atmospheric CO₂ being an indicator of the arterial-venous inorganic carbon difference. The metabolic rate is the internal-energy flux (here expressed as flux of inorganic carbon in the upper ocean) required by the system's machinery, i.e. community respiration. We propose that the pump rate is set externally by the annual cycle, at one beat per year per hemisphere, and that the autotrophic ocean adjusts its stroke volume and arterial-venous differences to modify the internal-energy demand, triggered by long-period astronomical insolation cycles (external-energy supply). With this perspective we may conceive that the Earth's interglacial-glacial cycle responds to an internal organisation analogous to that occurring in living beings during an exercise-recovery cycle. We use an idealised double-state metabolic model of the upper ocean (with the inorganic carbon/nutrients supply specified through the overturning rate and the steady-state inorganic carbon/nutrients concentrations) to obtain the temporal evolution of its inorganic carbon concentration, which mimics the glacial-interglacial atmospheric CO₂ pattern.

Keywords: deep-water formation, thermocline circulation, ocean physiology, Milankovitch cycles, arterial-venous concentration differences, organic and inorganic carbon, metabolic rate, glacial-interglacial cycle.

RESUMEN: UN ENFOQUE FISIOLÓGICO PARA LOS PROCESOS OCEÁNICOS Y LOS CAMBIOS GLACIALES-INTERGLACIALES DEL CO₂ ATMOSFÉRICO. – Un posible camino para el estudio de la homeóstasis fuera-de-equilibrio de la tierra es suponer que resulta de la organización de sistemas pulsátiles optimizados, análoga a aquella en seres vivos complejos. Bajo esta premisa parece natural examinar la organización de la tierra utilizando variables de tipo fisiológico. Aquí identificamos algunas de las principales variables del sistema circulatorio oceánico: tasa de bombeo del corazón, volumen de latido, diferencias arterio-venosas de carbono y nutrientes, suministro de carbono y nutrientes inorgánicos, y tasa metabólica. El volumen de latido es proporcional al transporte de agua hacia la termoclina y océano profundo, y las diferencias arterio-venosas ocurren entre las aguas profundas recientemente afloradas y aquellas altamente productivas de altas latitudes, con el CO₂ atmosférico siendo un indicador de la diferencia arterio-venosa de carbono inorgánico. La tasa metabólica es el flujo de energía interna (aquí expresado como flujo de carbono inorgánico en el océano superior) requerido por la maquinaria que sostiene el sistema, i.e. respiración total de la comunidad. Se propone que la tasa de latido está impuesta externamente, un latido por año por hemisferio, y que el océano autotrófico ajusta su volumen de latido y las diferencias arterio-venosas a cambios en la demanda de energía interna, inducido por ciclos de insolación astronómica de largo período (suministro de energía externa). Bajo esta perspectiva podemos concebir que el ciclo interglacial-glacial de la tierra responde a una organización interna análoga a la que ocurre en seres vivos durante un ciclo de ejercicio-recuperación. Se utiliza un modelo metabólico idealizado de dos estados para el océano superior (con el suministro de carbono/nutrientes inorgánicos especificado mediante la tasa de recirculación de aguas profundas y las concentraciones de carbono/nutrientes inorgánicos en estado estacionario) para obtener la evolución temporal de su concentración de carbono inorgánico, la cual mimetiza el patrón glacial-interglacial del CO₂ atmosférico.

Palabras clave: formación de aguas profundas, circulación termoclina, fisiología oceánica, ciclos de Milankovitch, diferencias arterio-venosas de concentración, carbono orgánico e inorgánico, tasa metabólica, ciclo glacial-interglacial.

WHY A PHYSIOLOGICAL PERSPECTIVE

The idea that the Earth has physiological behaviours has been endorsed by eminent naturalists, probably first in the 15th century by Leonardo da Vinci, who wrote that “the ocean fills the Earth’s body with an infinity of veins” with “water circulating as does the blood of animals”. James Hutton in the 18th century spoke of the Earth as a superorganism and compared the recycling of elements with the blood circulation, and one century later Vladimir Vernadsky proposed living matter as a geological force. Later on, other scientists recognised that the Earth and organisms have coevolved, but it was James Lovelock and Lynn Margulis (Lovelock, 1972; Margulis and Lovelock, 1974; Lovelock and Margulis, 1974) who brought to scientific debate the idea that our planet’s homeostasis is the result of life’s modulating force. Their Gaia hypothesis maintains that the Earth system may be understood as a living being, with biotic mechanisms that regulate its chemical cycles to maintain conditions suitable for life. Lovelock and others have searched for these self-regulating mechanisms (Watson and Lovelock, 1983; Charlson *et al.*, 1987), but a physiological characterisation is yet lacking.

It is perhaps time to resume da Vinci’s physiological perspective of the Earth, using today’s knowledge of its local and global organisation. Modern physiology aims to understand how living beings organise themselves towards an optimum thermodynamic state to maintain far-from-equilibrium homeostasis. Complex systems have global properties, not found in any of the component subsystems, which describe their organisation (Haken, 1983). Our fundamental premise is that the annually-pulsating insolation, the Earth’s ultimate energy-source, suits different far-from-equilibrium states (e.g. glacial and interglacial). And our working hypothesis is that the organisation of any Earth state, though occurring at many different spatial and temporal scales, may be described using global systems and variables of physiological type.

Let us consider the lithosphere as the original source of the ocean’s minerals, and the sun’s radiation as the ocean’s ultimate energy source. We view the active (in the sense that it may transform the sun’s energy) fraction of the Earth system as composed by atmosphere, biosphere and hydrosphere, all of them containing feedback processes that contribute to the Earth’s dynamic equilibrium. The hydrosphere has

by far the greatest mass and sustains the Earth’s circulatory system, which fully justifies talking about “ocean physiology”. The heat, carbon and nutrient fluxes in the ocean are of a similar order to those in the atmosphere and terrestrial biosphere, but their storage is much greater (Sigman and Haug, 2003; Sundquist and Visser, 2003). This gives the oceans a long temporal memory, capable of controlling the Earth’s processes on timescales of the order of millennia.

It may be argued that complex beings have an internal environment with numerous specialised interfaces and conduits for optimum exchange. While the ocean does not have such material surfaces its forcing and major ocean currents are quite localised so that it closely behaves, both in terms of contrasting water masses and property fluxes, as if those surfaces and conduits were present. In many instances there are steep density gradients that physically separate oceanic regions (Csanady, 2001; Wunsch and Ferrari, 2004), and major currents resemble close conduits for nutrient and carbon fluxes (Pelegrí and Csanady, 1991; Pelegrí *et al.*, 1996, 2006; Williams and Follows, 2003; Williams *et al.*, 2006).

One fundamental piece of information, and motivation, on ocean physiology comes from the seasonally changing hydrosphere, as emphasised by monthly compositions of infrared and colour satellite images. The Earth beats rhythmically, with intense spring/fall primary production at high/low latitudes and winter pumping of cold surface waters into the upper and deep oceans. This cycle of primary production and water pumping, externally imposed by the sun’s energy, drives the fluxes of mass, nutrients, carbon and energy through the ocean. The existence of natural pulsating frequencies is a fundamental characteristic of all living systems, which are thermodynamically optimised and internally far from equilibrium (Bejan, 1997), and we may anticipate that the annual cycle determines the physiological behaviour of the Earth system.

In this paper we first briefly review some key physiological processes, such as heart rate, cardiac output, arterial-venous differences and metabolic rate, and propose their counterparts in the Earth system. We then present a simple carbon model which assumes that the flux of dissolved inorganic carbon to the upper ocean switches between two different regimes. This conceptual model has the same simplicity as previous efforts (Calder, 1974;

TABLE 1. – Abbreviations for physiological variables used in the text, together with their definition, dimensions, characteristic units, and the system where they apply. Related symbols in the model equations are also included.

Variable	Definition	Dimensions	Characteristic units	System
a-v OD	arterial-venous oxygen concentration difference	oxygen per unit volume	ml-oxygen ml-blood	mammal
a-v DIC	arterial-venous dissolved-inorganic-carbon concentration difference	carbon per unit volume	mmol-carbon m ⁻³	Earth
a-v NO ₃	arterial-venous inorganic-nutrient concentration difference	nutrient per unit volume	mmol-nitrate m ⁻³	Earth
CO	cardiac output, $CO = HR \times SV$; Q in model equations	volume per unit time	ml-blood s ⁻¹ Sverdrup	mammal Earth
DIC	dissolved inorganic-carbon concentration	carbon per unit volume	mmol-carbon m ⁻³	Earth
ES	energy supply; for the Earth it is the result of inner supply $R - P$, and deep supply Qc_d , or $S = R - P + Qc_d = Q\gamma$ in model equations,	oxygen supplied per unit time carbon supplied per unit time	ml-oxygen s ⁻¹ kmol-carbon s ⁻¹	mammal Earth
HR	heart or pump rate; for the Earth it is set at one beat per year and hemisphere, the two hemispheres acting six months out of phase	beats per unit time	beats s ⁻¹ 1 beat year ⁻¹	mammal Earth hemisphere
MR	metabolic rate; for the Earth equals community respiration $PP - NCP$, or R in model equations	oxygen consumed per unit time carbon consumed per unit time	ml-oxygen s ⁻¹ kmol-carbon s ⁻¹	mammal Earth
NO ₃	inorganic-nutrient concentration	nutrient per unit volume	mmol-nitrate m ⁻³	Earth
NCP	net community production, or PP minus community respiration	carbon transformed per unit time	kmol-carbon s ⁻¹	Earth
OC	organic-carbon concentration	carbon per unit volume	mmol-carbon m ⁻³	Earth
PP	total or gross primary production	carbon transformed per unit time	kmol-carbon s ⁻¹	Earth
SV	stroke volume; for the Earth system CO and SV are numerically equal if the selected time unit is one year	volume pumped per unit beat	ml-blood beat ⁻¹ m ³ beat ⁻¹	mammal Earth
VC	deep-ocean inorganic-carbon consumption per unit time, $VC = HR \times SV \times a\text{-v DIC}$; $Q(c_d - c)$ in model equations	carbon per unit time	kmol-carbon s ⁻¹	Earth
VO ₂	oxygen consumption per unit time, $VO_2 = HR \times SV \times a\text{-v OD}$	oxygen per unit time	ml-oxygen s ⁻¹	mammal

Imbrie and Imbrie, 1980; Paillard, 1998; Paillard and Parrenin, 2004) but a very different justification, as it is inspired by how complex living beings switch between different metabolic states. We end up by summarising the novel elements in our approach and pointing to lines of future research. Table 1 presents several key physiological variables for mammals and their analogues for the Earth system, with definitions and units to be used throughout the manuscript.

Before proceeding, however, we ask our readers to keep in mind two main conducting concepts that apply throughout the manuscript. Later in the paper we will carefully discuss these ideas but, because of their importance, it is worth emphasising them from the very beginning. First, we will indistinctly talk of carbon and internal-energy fluxes. The fundamental biological process is the photosynthetic utilisation of solar radiation to fix carbon, but it is the respiration of this organic carbon by the whole community (autotrophs and heterotrophs) that determines the energy expenditure, or metabolic

state, of the Earth system. For this reason we will use both fluxes of inorganic and organic carbon as a measure of available or internal energy flux. This is a small fraction of the total incident radiation to the ocean (external energy flux), so any minor change in the external energy supply or in its transformation efficiency becomes very relevant to the internal energy fluxes. Second, we will consider changes during rather long spatial and temporal scales, aimed at examining glacial-interglacial changes. With this objective the time unit is one year, so we deal with annual averages, and the global ocean is simply divided into upper and deep oceans, with spatially constant properties for each compartment. The upper ocean consists of ventilated (surface and permanent thermocline) waters, with mean values typically varying from decades to millennia, while changes in the deep ocean are much slower. Glacial and interglacial periods will be interpreted to respectively correspond to basal (low-energy) and enhanced (high-energy) metabolic states of the Earth system.

KEY PHYSIOLOGICAL CONCEPTS

We begin by briefly reviewing some key physiological concepts in mammals (Campbell, 1990; Randall *et al.*, 2002; Guyton and Hall, 2005). This is necessary as we will later argue that the ocean system has variables with analogous functions, and use the physiological terminology when referring to them. There is no specific reason to choose mammals except perhaps because of their great complexity and extensive study. There may certainly be other species with a much closer Earth-like behaviour—probably plants holding both photosynthetic and respiratory processes. Nevertheless, our approach will prove useful to better understand the ocean's homeostatic organisation.

Mammals have a closed circulatory system that distributes oxygen and nutrients. The distribution motor is the heart, with low pressure gradients during the atrium-filling phase (diastole) and high pressure gradients during a relatively short ventricle-contracting and blood-pumping phase (systole). The four-chambered heart (two atria and two ventricles) supports a double-circulation system. The right side of the heart receives deoxygenated blood and pumps it via the pulmonary branch to capture oxygen. The left side restores pressure and delivers oxygenated blood to all parts of the body through the systemic branch, including the stomach and intestines where it incorporates nutrients. The mean residence time of blood parcels in the pulmonary branch is typically one-tenth of that in the systemic branch. In humans, for example, these are respectively about 5 seconds and one minute. These times, together with the organs' contact surfaces, are set to optimise the transfer of oxygen from the lungs (fast air diffusion) and nutrients from the intestine (slow liquid diffusion). The heart contraction rate is set locally, through pacemaker cells located in the sinoatrial node, which respond rapidly to impulses of the nervous system and more slowly to hormones from the endocrine system. They have high impedance so only small currents are necessary to change their membrane potential (action potential), and consequently the contraction rate.

The metabolic rate MR is the energy per unit time used to sustain all body functions. In steady state the MR equals the energy supply through biomass oxidation, so MR is commonly measured in terms of oxygen consumption, VO_2 (ml-oxygen s^{-1}). An organ's VO_2 is the product of heart rate HR (heart cycles per unit time, beats s^{-1}), stroke volume SV (blood

pumped by either ventricle during contraction, ml-blood $beat^{-1}$), and its arterial-venous oxygen difference, a-v OD (O_2 change between the arriving and departing blood, ml-oxygen ml-blood $^{-1}$), i.e. $VO_2 = HR \times SV \times a-v \text{ OD}$. Total VO_2 increases from rest to exercise through increases in HR, a-v OD, and SV, with its maximum value being typically one order of magnitude greater than the rest value, though this depends on age and training. Another useful quantity is cardiac output, CO (ml-blood s^{-1}), which gives the flow pumped by either ventricle per unit time, i.e. $CO = HR \times SV$. Table 1 summarises the main physiological variables involved in the supply of oxygen, and metabolic expense, for mammals.

In mammals, as for all life, adenosine triphosphate ATP molecules are the immediate energy source that maintains cellular work. As exercise begins, there is a time delay before the aerobic (mitochondrial glucose transformations) ATP production (VO_2) can meet the new MR. This oxygen deficit requires the utilisation of reserve ATP molecules in cells (phosphagen energy system). When activity is so large that stored ATP is used and mitochondrial supply cannot keep pace, then a period of dominant anaerobic (glycolysis) ATP production follows, which generates lactic acid as a by-product. In humans, for example, maximal muscle power is sustained by ATP reserves for about 3 seconds, by the phosphagen system for nearly 10 seconds, by the glycogen-lactic acid system for about 1.5 minutes, and by the aerobic ATP-production system as long as nutrients last.

As exercise ends, a time of recovery begins, during which oxygen consumption exceeds the power (MR) requirements. This oxygen debt is greater, and lasts much longer, than the oxygen deficit as it involves not only the reconstitution of the phosphagen system but also that of the lactic acid system and the replenishment of oxygen stores (in lungs, blood and body fluids, and muscle fibres) (Fig. 1a). During the exercise-recovery cycle the a-v OD changes are roughly paralleled by a-v glucose and lactate differences (Ide *et al.*, 2000; González-Alonso *et al.*, 2004) (Fig. 1b).

THE OCEAN'S PUMP RATE, STROKE VOLUME AND CARDIAC OUTPUT

The predominant signal in Life and Earth processes is the annual cycle, caused by the Earth's revo-

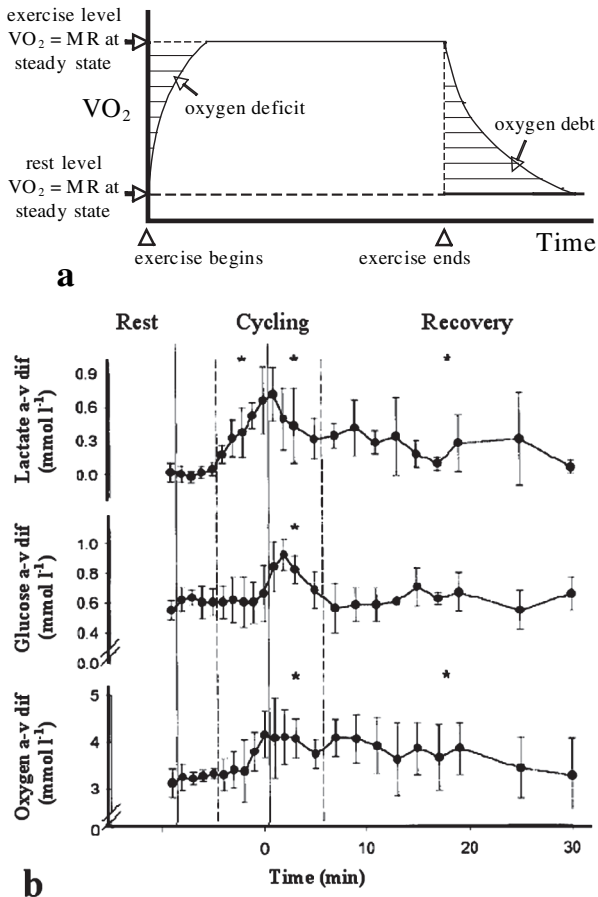


FIG. 1. – (a) Schematic illustration of metabolic rate (MR) and oxygen consumption (VO₂) per unit time during an exercise-recovery cycle. MR is shown as a step function (dashed line), and VO₂ follows MR with some time lag (solid line). (b) Each organ has analogous patterns in oxygen and nutrient a-v differences. Here we show oxygen, lactate, and glucose a-v differences in the human brain following the onset of heavy exercise (dashed vertical line) and after its termination. Adapted from Ide *et al.* (2000).

lution around the sun with its tilted rotation axis. The daily cycle is essential for primary production but all major biological processes (primary production and respiration) and physical processes (surface mixed-layer evolution and recirculation of surface waters through both the permanent thermocline and the deep ocean) are modulated by the seasonal cycle. The dominance of seasonality in all major oceanographic (biological, chemical and physical) processes indeed sets the Earth's HR to a constant value of one beat per year, so that for our physiological description of the ocean we have the same figures when referring to transports per beat (SV) or per year (CO). Hereafter we will express the Earth's annual-average CO using the standard oceanographic unit for water transport, the Sverdrup (1 Sv = 10⁶ m³ s⁻¹). In this section we concentrate on the physics of the ocean circulatory system, forced at the air-sea interface. In Table 1 we

find several key variables for the Earth's circulatory system, presented using physiological terminology, to be used in this and the following sections.

Water is deep-convected (transferred to the deep ocean) rather suddenly during winter, following intense surface cooling, in what constitutes the start of the thermohaline circulation or global conveyor belt. North Atlantic Deep Water is formed in the high-latitude North Atlantic during winter, at an annual-average rate of some 13 to 20 Sv, from where it flows to the southern hemisphere (Schmitz, 1995; MacDonald and Wunsch, 1996; Ganachaud and Wunsch, 2000). Meridional overturning also takes place on the continental shelves around Antarctica, where some 8 to 24 Sv (annual-average values) of nutrient and carbon-rich Antarctic Bottom Water and Lower Circumpolar Deep Water are formed (Broecker *et al.*, 1998; Orsi *et al.*, 1999; Ganachaud and Wunsch, 2000). These cold deep waters are dense enough to drive the long (several hundred years to millennia) journey to the Indian and Pacific via the Antarctic Circumpolar Current (Schmitz, 1995; MacDonald and Wunsch, 1996; Talley *et al.*, 2003). The recirculating flow exchanges heat, oxygen, carbon and nutrients with the upper ocean mainly through equatorial upwelling, and also through eastern boundary upwelling and slow widespread diapycnal (across-density surface) diffusion, and eventually returns to the source regions (Figs. 2a,b,c). The southern areas of deep-water formation are reached by the Circumpolar Current via upwelling (Orsi *et al.*, 1999), but replacement of northern waters is more complex. Relatively shallow Subantarctic Mode Waters, formed in the Indian Ocean, and deeper Antarctic Intermediate Waters, principally formed in the eastern South Pacific, reach the tropical Atlantic region, the former via the Agulhas Current (Sarmiento *et al.*, 2003; Williams *et al.*, 2006) and the latter along the western boundary of the South Atlantic (Saenko *et al.*, 2003), where vertical mixing and equatorial upwelling takes place (Gouriou and Reverdin, 1992; Sarmiento *et al.*, 2003). These upwelled waters are then advected west by the equatorial current system and follow north along the western margin via the boundary currents (Rintoul and Wunsch, 1991; Williams *et al.*, 2006; Talley *et al.*, 2003) (Fig. 2d).

Additionally, surface water is subducted (transferred to the permanent thermocline) in all subtropical gyres and the meridional portion of the adjacent subpolar gyres (Figs. 2a,b,c). This occurs as a result of downward Ekman (wind-induced) pumping, im-

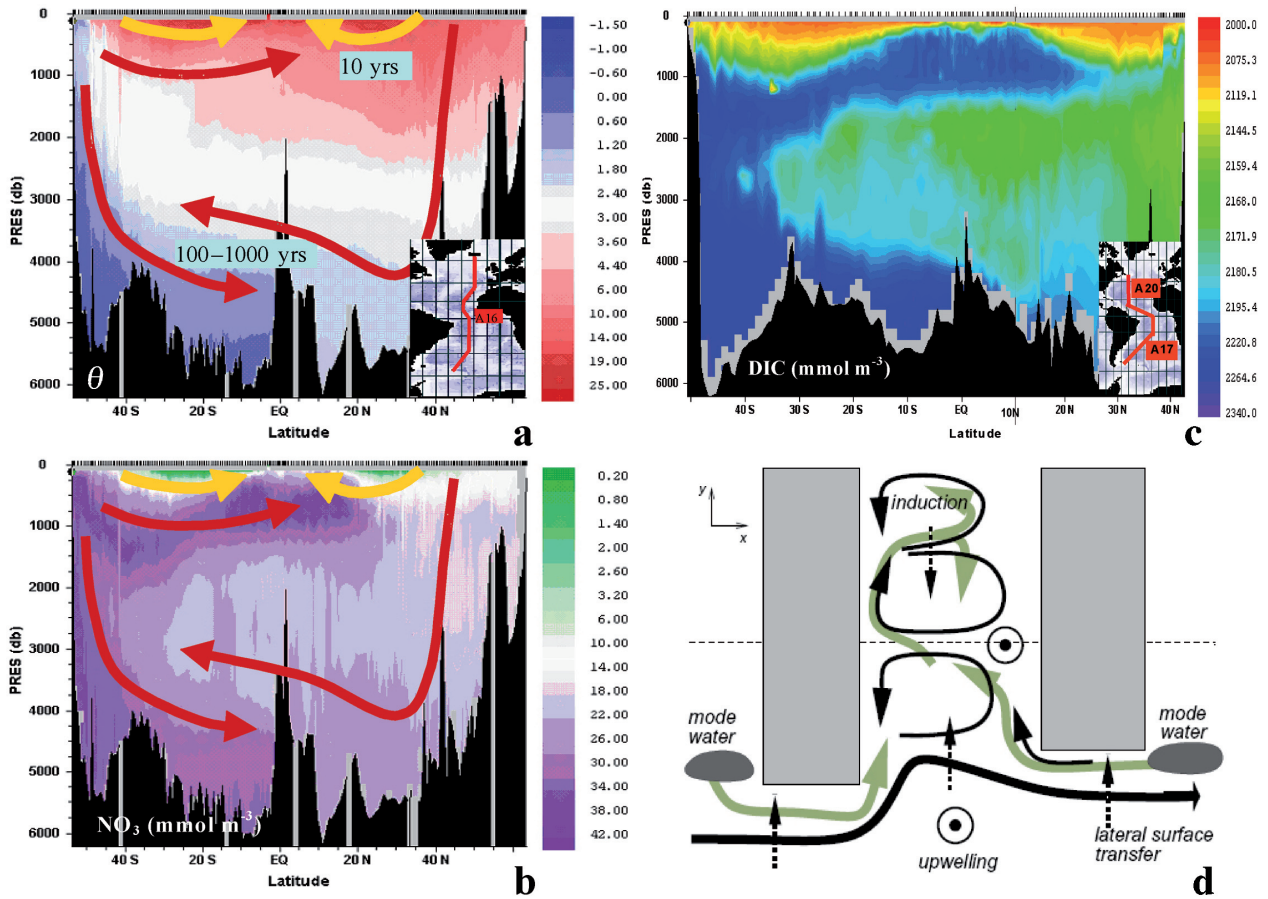


FIG. 2. – The data shown in (a) and (b) correspond to WOCE’s line A16, occupied in spring 1989 (southern and central portions) and summer 1989 (northern portion), while those shown in (c) correspond to WOCE’s lines A20 and A17, occupied in summer 1997 and winter 1994, respectively. (a) Potential temperature and (b) nitrate concentration distributions, over which we have superimposed some gross circulation patterns and characteristic recirculation times. (c) Distribution of DIC; it is like nitrate but inorganic carbon is clearly non-limiting. (d) Return paths in the upper ocean to the deep-convection regions. Sub-Antarctic mode waters (gray shaded) approach the surface waters in the equatorial region and, in the North Atlantic, join the upper gyre recirculation (black solid arrows) to reach the northern deep-water formation regions. The black dashed lines depict Ekman transfer from high latitudes to the subtropical gyres. Reproduced from Williams *et al.* (2006).

mediately after the formation of the winter mixed-layer (Stommel, 1979; Kawase and Sarmiento, 1985), and takes of the order of ten years to recirculate epipycnally (on density surfaces) around the subtropical gyres (Reid, 1994; Lozier *et al.*, 1995). During this journey organic materials become progressively remineralised, so that the concentration of inorganic carbon and nutrients increases (Kawase and Sarmiento, 1985; Louanchi and Najjar, 2000). When these waters complete their subtropical trip and return to the high-latitude surface layers, they are ready to sustain the new spring production cycle (Pelegrí and Csánady, 1991; Rintoul and Wunsch, 1991; Pelegrí *et al.*, 1996, 2006; Williams and Follows, 2003; Williams *et al.*, 2006) (Fig. 2d). This circuit requires only a minor supply of new nutrients to cover for losses to the deep ocean (Sigman and Haug, 2003).

The above description shows (i) that atmospheric seasonal forcing at the ocean surface sets the pumping

for both upper and deep waters, with a winter high-pressure (systole) escaping phase from temperate and high-latitude regions and a continuous low-pressure (diastole) recirculation back to the surface layers, and (ii) that water parcels follow two dominant oceanic recirculation paths, a long-slow deep recirculation and a short-fast recirculation through the ventilated waters (surface and permanent-thermocline, hereafter upper ocean) (Fig. 3a). For both the Earth and mammals, the driving forces are surface-force gradients. In mammals these are pressure differences, set mechanically via heart pumping. In the Earth’s systemic branch these are also pressure differences, caused by winter cooling and density excess in the formation regions. In the Earth’s pulmonary circuit, however, the driving forces are wind-stress gradients, which set up Ekman pumping and water subduction.

From a physiological perspective we could envision the Earth’s circulatory system as driven by two

separate pumps (one per hemisphere) that operate alternately, with a six-month phase difference, each one fluxing the two circuits. The two pumps would share one predominant atrium (the equatorial ocean) and each one would have two ejecting ventricles (Fig. 3b). For our purposes we may consider them to constitute one double-pump with annual periodicity and combined transport. The SV for the deep branch is somewhere between 20 and 40 Sv, while that for the upper branch reaches up to 100 Sv per subtropical gyre. These different strokes, combined with the unequal volumes, result in the short/long recirculation times for the upper/deep circuits.

NUTRIENT AND CARBON SUPPLY TO THE UPPER OCEAN

Life on Earth is only possible thanks to the sun’s radiation, except near hydrothermal vents, so the Earth is essentially a photo-autotrophic system. Over a certain geographic region, or even as a whole during some time period, the Earth may behave heterotrophically but its long-term homeostatic equilibrium depends on its capacity to transform the sun’s energy. For such a system the key physiological variables are dissolved inorganic carbon DIC (carbon m^{-3}) and nutrient concentrations, hereafter to be represented by nitrate concentration NO_3 (nitrate m^{-3}).

The upper recirculation sustains the productive euphotic layer and may be interpreted as the ocean’s pulmonary circulation branch. High levels of primary production (carbon ingassing, oxygen outgassing, and nutrient utilisation) occur during spring in subpolar regions following wintertime mixing and epipycnal nutrient resupply (Pelegrí and Csanady, 1991; Pelegrí *et al.*, 1996, 2006; Williams and Follows, 2003; Williams *et al.*, 2006), and during autumn in tropical regions following Ekman (wind-induced) pumping and diapycnal mixing (Pelegrí and Csanady, 1991; Signorini *et al.*, 1999). The pulmonary branch is very efficient thanks, first, to along-path regeneration of both inorganic nutrients and carbon (Kawase and Sarmiento, 1985; Louanchi and Najjar, 2000) and, second, to O_2 and CO_2 exchange with the atmosphere that sustains both photosynthesis and respiration of marine organisms (Najjar and Keeling, 2000; Takahashi *et al.*, 2002). Despite its efficiency, it has some nutrient and carbon losses during the formation of deep waters and as hard falling particles (Sigman and Haug, 2003), so the NO_3

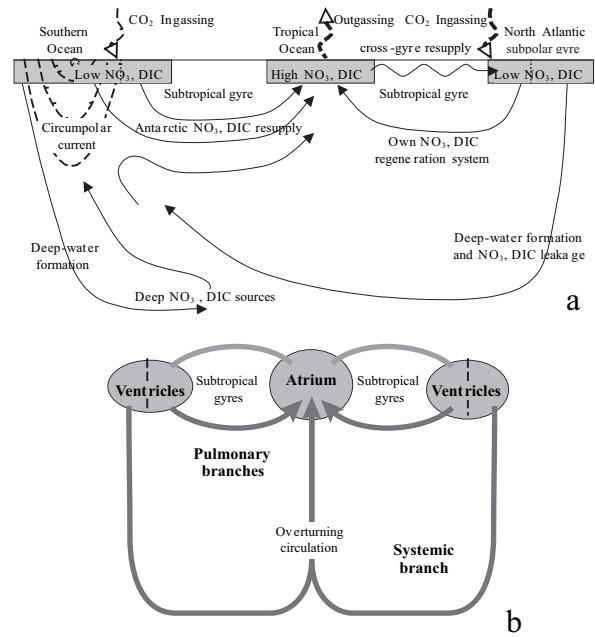


Fig. 3. – (a) Major mass, nutrient, and carbon pathways connecting the upper and deep oceans. Most deep water is formed at high latitudes in the Atlantic, in what constitutes the start of the overturning circulation, and returns to the near-surface ocean in the Antarctic shelf and equatorial regions. Additionally, all subtropical gyres hold very efficient production-remineralsation processes in the upper-ocean recirculation. (b) Idealised physiological representation of the ocean circulation as an out-of-phase double-pump system, each pump containing three-chambers and sustaining a double-circuit. Each pump flushes to an (almost) independent pulmonary circuit (upper ocean) and to one common systemic circuit (deep ocean).

and DIC levels are maintained through input of inorganic carbon and nutrients from the deep systemic branch (Fig. 3a).

Deep waters reach the upper branch mainly in equatorial regions, bringing high concentrations of inorganic nutrients and carbon. The upper ocean then uses some of the abundant CO_2 and most available NO_3 to sustain an optimum level of near-surface productivity. Most nutrients in the upper ocean recirculate through the euphotic zone, where they become nearly exhausted, so we may imagine their upper-ocean maximum concentrations as the arterial-venous nutrient differences (a-v NO_3) for the primary production ocean ‘organ’. Carbon follows the same water-paths as nutrients but may efficiently reach all surface oceans via the atmosphere, the equilibrium sea-atmosphere flux resulting from the CO_2 partial pressures in the surface waters and low atmosphere (Takahashi *et al.*, 2002). The atmosphere short-circuits the supply to the euphotic zone, with outgassing in equatorial regions (after equatorial upwelling of high DIC intermediate waters) and ingassing at high latitudes (biological and physical pumps), so carbon is non-limiting for primary production.

It is important to emphasise that the ultimate source for the carbon abundance in the upper ocean is not the atmosphere but the deep ocean, the surface-ocean DIC setting the low-atmosphere CO₂ concentration. The temporal scales for horizontal motions in the atmosphere are relatively short so, for this study, we view the sea-surface atmospheric CO₂ as spatially constant, roughly proportional to the average between the outgassing (c_{out}) and ingassing (c_{in}) sea-surface DIC values. This average may be written as $(c_{out} + c_{in})/2 = (c_{out} - c_{in})/2 + c_{in}$ which means that if c_{in} changes little compared with c_{out} , then the atmospheric CO₂ is roughly proportional to the difference between the outgassing and ingassing regions, an indicator of the a-v carbon difference of the euphotic zone (a-v DIC).

The amount of carbon and nutrients that reach the upper ocean is set by the combination of two factors: their deep-ocean concentrations and the pathway and intensity of the deep recirculation. The evidence on geological changes in deep-ocean concentrations is ambiguous—for a review see Sigman and Haug (2003)—but it seems clear that the deep recirculation has intensified during interglacial periods (Imbrie *et al.*, 1992; Sigman and Boyle, 2000). Today's large rate of deep-nutrient supply is likely responsible for the relatively high present levels of unused nutrients in high-latitude and upwelling regions (Conkright *et al.*, 1994; Williams and Follows, 2003), which leak to all anticyclonic subtropical gyres (Pelegrí and Csanady, 1991; Pelegrí *et al.*, 1996, 2006).

ASTRONOMICAL PACEMAKERS

The annual HR sets the tempo of the fluxes of heat, mass, nutrients, and carbon throughout the ocean but it is essential to understand what dictates their intensity. Given the dominance of the seasonal processes in the Earth's biogeochemical balances, we expect the intensity of these fluxes to be linked to the solar radiation annual cycle. For example, the ocean changes its heat content principally through the seasonal cycle in the subtropical and subpolar regions (Oort and Peixoto, 1994; Antonov *et al.*, 2004), i.e. without seasons the ocean-atmosphere exchange would be dramatically reduced. Before looking into the ocean's metabolic rate let us briefly review what parameters are truly astronomical pacemakers (Hays *et al.*, 1976), as they control the strength of the seasonal cycle, or seasonal contrast.

A physiological perspective alerts us that setting up the action potential in pacemaker cells will have minute power requirements as compared with the energy involved in the metabolic response. Hence, we expect that the seasonal contrast, acting as the Earth's action potential, has to overcome some energy threshold whose value is much less than the system's energetic response. Milutin Milankovitch showed that the spatial distribution and amplitude of the annual insolation cycle depends on eccentricity, obliquity and precession. The annually integrated insolation has experienced very small changes during the last million years, within about 0.2% of today's value, but seasonal variations have been much more significant. All three parameters contribute to a certain degree, depending on latitude, to modifying the seasonal contrast (Hays *et al.*, 1976; Berger, 1978; Williams *et al.*, 1998).

Obliquity, the angle between the Earth's rotation axis and the ecliptic plane, has varied as much as 2.5° during the last million years, with an average periodicity of about 41 ka (1 ka = 1000 yr). Obliquity modifies the angle of incidence of the solar beam so that its maximum effect on the seasonal contrast takes place at high latitudes, a 2° change at 65°N modifying the seasonal irradiance by 5%. A 41 ka cycle dominated the climate record between about 3000 and 800 ka ago, suggesting that during such a period of relative low ice coverage obliquity was a key factor for setting the glacial-interglacial changes (Raymo and Nisancioglu, 2003).

Eccentricity is a measure of the Earth's orbit ellipticity. The current eccentricity ($e = 0.016$) results in a 7% annual increase in insolation from aphelion (the point in the Earth's orbit farthest from the sun) to perihelion (the point closest), but variations during the last ca. 800 ka (e as large as 0.05) have caused changes in seasonal insolation of up to about 20%. Eccentricity, with cycles of approximately 100 and 412 ka, has set the dominating 100 ka temperature and carbon cycle during this period (Hays *et al.*, 1976; Imbrie *et al.*, 1992; Raymo, 1997; Ridgwell *et al.*, 1999; Shackleton, 2000).

The occurrence of glacial-interglacial transitions, however, has likely been triggered by precession, which indicates the direction of the Earth's rotation axis in space and sets the season at perihelion and aphelion. The axis orientation has cycles at about 19 and 23 ka, with a mean period of about 21 ka during the last million years. The timing in physical and biogeochemical processes (e.g. deep-water formation

and primary production) is very important to planetary mass and energy fluxes (Nicolis, 1982). The maximum rate of deep-water formation is probably related to the occurrence of maximum eccentricity during winter (Raymo, 1997; Ridgwell *et al.*, 1999), so precession could be responsible for triggering SV changes in the dominant ventricle (hemisphere) of the ocean's double-pump system (Fig. 3b).

THE OCEAN'S METABOLIC RATE

The Earth's system operates thanks to the incident solar energy. About 30% of this energy, corresponding to a combined Earth's albedo of 0.3, is reflected or scattered back to space, but the remaining 70% is transformed within the system by a myriad of physical processes before radiating out of the Earth (Gill, 1982; Csanady, 2001). Only a small fraction of this transformed energy, somewhere between 0.1 and 1% (Platt *et al.*, 1989), becomes available to phytoplankton and phototrophic bacteria for photosynthesis. As an extension of Margalef's (1978) ideas, we identify external energy as that supporting the operation of the whole system, and internal energy as the small fraction that becomes available to the whole community through the photosynthetic conversion efficiency.

Life on Earth relies on its photo-autotrophy, which uses the internal energy to transform inorganic into organic matter, but the system's biological machinery can only sustain itself through oxidation of this organic carbon. The exploitation of solar energy to transform carbon justifies using carbon as a measure of internal energy, either as potentially available energy (DIC) or as readily expendable energy (organic carbon). The upper-ocean metabolic rate (MR) is a key time-dependent variable that measures the organic carbon (and nutrients) actually used by the system to maintain its metabolic activity; it is an internal-energy flux here expressed as carbon s⁻¹ (recall that the upper ocean includes the surface and permanent thermocline waters). MR differs from gross primary production (or simply primary production PP) in that the latter includes inorganic carbon transformed for plant growth and storage. PP is the total carbon fixed through photosynthesis and that remaining for community growth, after subtracting the costs for community respiration (autotrophs and heterotrophs), is net community production (NCP) (Platt *et al.*, 1989). MR would hence represent the difference between PP and NCP, i.e. the energy used (carbon respired) by the upper-ocean community to sustain its life processes (Fig. 4).

For the upper ocean, we must keep in mind that carbon is never limiting thanks to the atmospheric

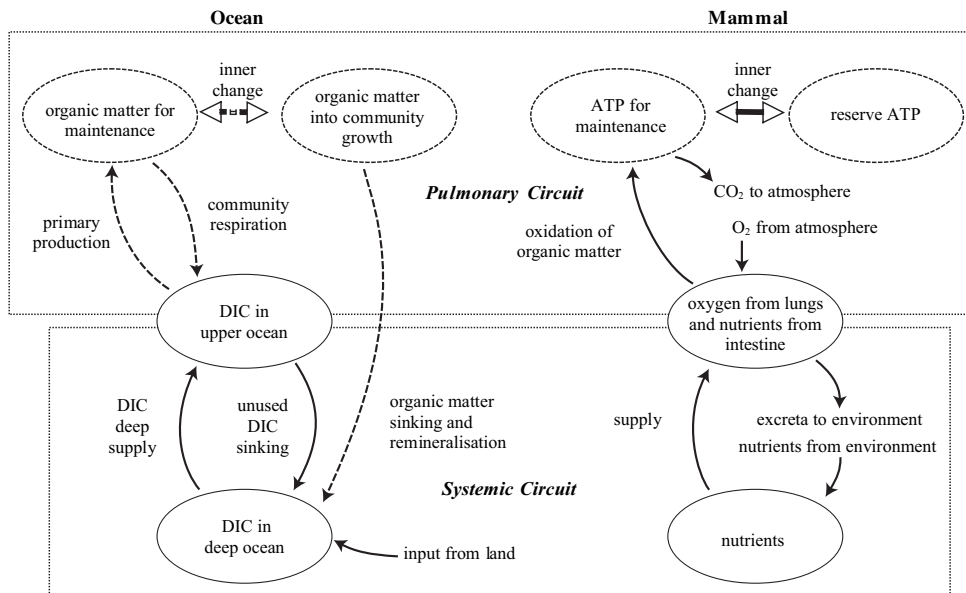


FIG. 4. – Schematics of the fluxes (arrows) and reservoirs (ellipses) of energy for mammals (right) and the ocean (left), drawn to emphasise the similar energy-transformation patterns in mammals and the Earth system. The former are open systems that exchange gases and nutrients with the environment, while the Earth may be thought as a closed system with no net carbon input/output. For the Earth energy fluxes are expressed as carbon fluxes: solid arrows represent fluxes of inorganic carbon and dashed arrows indicate conversion between inorganic and organic forms. For both ocean and mammals the metabolic rate is the temporal rate of change of the maintenance reservoir, in the case of the upper ocean given by $MR = PP - NCP$. Abbreviations are as in Table 1.

short-circuit, and nutrient availability is the real restraint on the internal-energy fluxes. For this reason we could perhaps relate MR to the utilisation of inorganic nutrients, rather than carbon, but we feel that the latter is a more natural “energetic” unit as the photosynthetic fixation of carbon is the fundamental biologic process that transforms the sun’s energy. Therefore, MR is quantified through the net utilisation of inorganic nutrients in the euphotic regions, multiplied by the appropriate carbon/nutrient Redfield proportionality ratio.

The system’s MR is maintained by the photosynthetic transformation of inorganic matter, coming both from the upper-ocean reserves and from inner/deep supply. An inner source of inorganic nutrients (and carbon) comes from its own MR (respiration of organic reserves). If MR is less than PP, then there is a net transformation of inorganic into organic nutrients in the upper ocean. The upper-ocean inorganic reserves are very limited, as most of these nutrients come from remineralisation during the upper-thermocline journey (Kawase and Sarmiento, 1985; Louanchi and Najjar, 2000), so this situation would only be sustainable for quite short times (relative to the glacial-interglacial 100 ka period). Alternatively, MR could exceed PP only by relying on the upper-ocean organic reserves, again a time-limited situation.

The system could actually operate indefinitely if all PP was used to sustain its MR (zero NCP), but our earlier discussion has shown that there are organic and inorganic leaks to the deep ocean (deep-water formation). This suggests that the Earth’s upper-ocean energy expenditure will oscillate between two states, glacial and interglacial, characterised by different deep-ocean supply of inorganic nutrients that are capable of sustaining quite distinct MR. Since the Earth’s HR is constant, this deep inorganic-nutrient supply depends on the meridional overturning rate (systemic SV) and the concentration of deep upwelled waters. Not all inorganic carbon and nutrients supplied to the upper ocean are actually utilised to maintain the MR, as some recirculate back to the deep ocean. The inorganic-concentration differences between deep upwelled-waters and surface deep-convected waters sets the a-v differences for the upper ocean, which for inorganic carbon (a-v DIC) are proportional to the annual-global mean atmospheric CO₂ concentration.

For mammals the MRs of basal or enhanced states are typically calculated from the corresponding steady-state consumption of oxygen, which

assumes that all necessary energy expenditure is eventually supplied by aerobic ATP production. An analogous perspective for the upper ocean suggests that the MR of either glacial or interglacial periods is to be reached after a long-enough continued level of inorganic carbon and nutrient supply. As the meridional overturning circulation increases from glacial to interglacial periods (Imbrie *et al.*, 1992; Sigman and Boyle, 2000; Sigman and Haug, 2003), it appears natural to associate these changes with those occurring between basal and enhanced states. In next section we will see that for a steady-state upper ocean, i.e. with constant organic and inorganic carbon/nutrient budgets, NCP is equivalent to the new production supplied by the deep-ocean inorganic nutrients/carbon that become incorporated in the upper ocean, $VC = HR \times SV \times a-v \text{ DIC}$. In this situation the new-deep carbon/nutrients supply also equals the loss of organic carbon/nutrients from the upper to the deep ocean (in analogy to the equivalence between long-term NCP and new production in the euphotic zone, Platt *et al.*, 1989).

Our starting premise was that the Earth’s homeostasis is, as for all living beings, the outcome of an optimal thermodynamic organisation, i.e. the complex system organises itself in one of many optimum states or attractors (Haken, 1983). The discussion in last section suggests that during the last ca. 800 ka the astronomically-induced variations in seasonal contrast, specifically the amplitude of the seasonal change in the meridional gradients of insolation, may have caused a 100 ka action-potential cycle. The physiological analogy endorses the idea that, as a result of this cycle, the upper ocean has switched between two different energetic states. These two states are characterised by quite different thermohaline-recirculation rates (slow/fast during glacial/interglacial periods), which require dissimilar ocean heat-absorption rates to transform deep into surface waters (external energy), and by very distinct metabolic rates, as a result of different supply of deep-ocean inorganic nutrients (internal energy).

A sustained change in oceanic heat-gain, through a modification in the seasonal contrast for a sufficient number of years, would produce two key (physical and biological) direct effects. The first effect (physical) would be a modification in the rates of deep-water formation and recirculation in the upper ocean. The important role of high-latitude insolation on the intensity of the deep-ocean thermohaline circulation (systemic SV) has already been proposed by many

researchers, and there is conclusive evidence on the reduction of the meridional overturning circulation during glacial periods (e.g. Imbrie *et al.*, 1992; Labeyrie *et al.*, 1992). But such variations in heat gain would also modify the winter meridional temperature gradients in both the atmosphere and the upper ocean. Changes in atmospheric temperature gradients would affect the surface winds and water pumping into the permanent thermocline (pulmonary SV), to be accommodated by modified temperature gradients and geostrophic velocities in the upper ocean. Such meridional temperature gradients would increase during glacial periods, resulting in a swifter thermocline circulation and a reduction of the pulmonary circulation time (as proposed by Sigman and Boyle, 2000) that would reach a maximum by the time of the glacial-interglacial transition.

The second effect (biological) is that changes in oceanic heat-gain could likely modify bacterioplankton heterotrophic production (Pomeroy *et al.*, 1991; Rivkin and Legendre, 2001; La Ferla *et al.*, 2005) and the efficiency of nutrient and carbon recycling in the pulmonary circuit. Most efficient recycling may occur following those astronomical conditions that lead to an increase in ocean heat gain, at the beginning of an interglacial period. Del Giorgio and Duarte (2002) have compiled in situ observations to conclude that oceanic respiration exceeds primary production, despite expectations of an increased biological pump as a result of today's greatly increased atmospheric carbon concentrations, and suggest that this may be the result of efficient recycling of ancient dissolved organic carbon as a response to temperature-enhanced respiration. The ocean has some 700 Pg of dissolved organic carbon, about half of it in the upper ocean (Sundquist and Visser, 2003), and today's differences between respiration and production (about 6 Pg C yr⁻¹, with large error bars, according to Del Giorgio and Duarte, 2002) indicate that this reservoir may have been much greater in the past, at the beginning of this interglacial period. A plausible conclusion is that remineralisation of dissolved organic matter in the upper ocean could sustain an enhanced level of primary production, with no need to increase the supply of deep inorganic nutrients, during a time scale of the order of several hundred years. This argument clearly does not exclude other possible causes for an expansion of dissolved inorganic matter at the start of an interglacial rise. Remineralisation of labile organic matter would act on time scales shorter than that of ancient organic

materials, and other processes, such as the erosion of continental margins by sea-level rise and enhanced terrestrial sedimentation, could take much longer. These distinct processes could supply the required inorganic nutrients at different time scales, in a sense emulating those different systems that supply ATP to exercising mammals.

The way mammals use anaerobic ATP to satisfy a sudden increase in energy demand, and build up ATP reserves under situations of low-energy requirements, is illuminating (Fig. 4). A comparable ocean organisation would involve (i) major sustained transformation between organic and inorganic nutrients/carbon, with the inorganic forms playing the role of aerobic ATP and the organic ones mimicking the ATP reserves and anaerobic sources, and (ii) an efficient flux of these inorganic forms to the euphotic layers, the productive part of the system. At the glacial-interglacial transition the recycling of organic matter would reach a maximum, as a result of the rapid increase in temperature and the still low upper-ocean f-ratio (the ratio between primary production using new inorganic nutrients that enter the upper ocean, and total primary production) (Platt *et al.*, 1989), and the thermocline circulation would still remain fast enough to ensure an efficient distribution of remineralised matter within the upper ocean. These processes would rapidly raise the concentrations of inorganic carbon and nutrients in the upper ocean (and consequently in the euphotic zone), leading to a state capable of supporting high internal-energy requirements. This state would eventually be maintained by the thermohaline recirculation, as it became vigorous enough (during the interglacial period) to bring greater amounts of deep inorganic nutrients to the upper ocean.

A SIMPLE MODEL OF THE UPPER-OCEAN CARBON AND NUTRIENT CONTENT

Let us view the ocean system as switching between two different metabolic states: a rest or basal state (glacial) that lasts most of the time and an exercise or enhanced state (interglacial) induced by some appropriate astronomic conditions. After sufficient time at rest the system would be in steady state, its MR being sustained by a relatively slow recirculation of deep-ocean nutrients. Imagine now an enduring change in ocean heat-gain, possibly induced by a sustained variation in the seasonal contrast as

described above, which triggers a proportional non-linear change in the ocean's MR. During the transition from rest to exercise, the initial supply of deep inorganic nutrients represents an insufficient energy source, so the enhanced MR relies on increased recycling of organic reserves (the f-ratio decreases): respiration temporally exceeds primary production and the ocean becomes heterotrophic. This situation cannot last indefinitely, because of the limited reservoir of dissolved organic matter in the upper ocean and losses to the deep ocean. However, the timing is so good (as for any optimised system) that as exercise continues the meridional overturning circulation increases (following appropriate astronomical forcing) and the deep-ocean nutrient inorganic supply matches the MR. This change in deep supply takes place through an intensification of the thermohaline circulation (systemic SV) and/or an increase in the nutrient concentrations reaching the upper ocean, until the high-energy requirements are satisfied. If the exercise MR remains constant for a sufficiently long time, then the system eventually reaches an enhanced autotrophic steady state. In this state PP exceeds MR (community respiration) exactly by the utilisation of new nutrients (expressed as carbon s⁻¹, proportional to the deep supply of inorganic nutrients less the nutrients recirculated back to the deep ocean), the amount also being equal to the sinking rate of organic carbon. During the opposite transition, from high to low metabolic states, the deep energy flux again lags behind the metabolic demand, so an initial excess supply of inorganic nutrients causes PP to far exceed MR (beyond the amount of organic carbon transferred to the deep ocean), resulting in the build-up of organic reserves. Eventually the deep supply diminishes and the basal autotrophic steady level, with low energy requirements, is once again attained.

We may exploit these ideas to construct an idealised carbon model for the upper-ocean DIC variations, and the equilibrium atmospheric CO₂ (Fig. 5). In a sense it may be considered as an energetic model, as the carbon fluxes and transformations are a measure of the internal energy supply to the upper ocean. Although the concentrations of nutrients and carbon display substantial seasonal and spatial differences throughout the upper ocean, in our simplified model we will ignore such differences and look at the long-time (glacial scale) behaviour of the mean (annual and upper-ocean average) concentrations. The model may also be applied for nutrients in the upper ocean, which are indeed the limiting factor

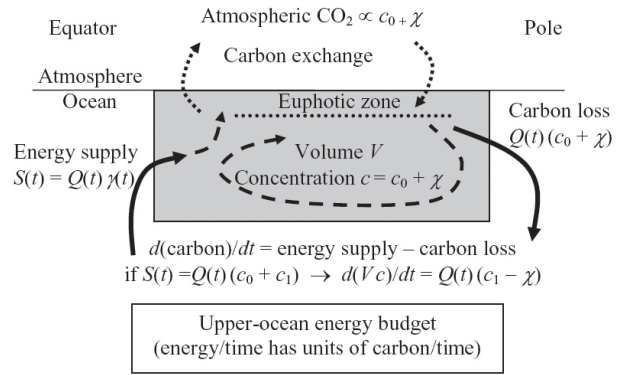


FIG. 5. – Schematics of the upper-ocean dissolved inorganic carbon balance in our idealised model.

controlling primary production, but we will focus on predicting the DIC glacial-interglacial pattern as this can be compared with observations of atmospheric CO₂. The model is extremely simple as it imposes the supply of inorganic carbon (proportional to the limiting nutrients), both by input from the deep ocean and by the upper-ocean remineralisation rate. Further, it does not explicitly consider any carbon solubility effect arising from changes in temperature and alkalinity.

We write down simple equations for the mean upper-ocean concentrations of dissolved inorganic carbon (DIC), c , and dissolved organic carbon, c_r :

$$\frac{d(cV)}{dt} = R - P + Q(c_d - c) \quad (1)$$

$\xrightarrow{\text{steady state}} P - R = Q(c_d - c)$

$$\frac{d(c_r V)}{dt} = P - R - Q c_r \xrightarrow{\text{steady state}} P - R = Q c_r, \quad (2)$$

where $Q(t)$ is the overturning rate (systemic CO), V the upper-ocean volume, c_d the DIC of the deep ocean, and R and P the remineralisation and primary production of the upper ocean, respectively (note that we could also think of the c symbol as indicating a concentration of any major nutrient). The left-hand-side terms in Equations (1) and (2) represent, respectively, the changes in the reservoir of inorganic and organic carbon in the upper ocean. Units in these equations are as shown in Table 1, with R and P having units of MR. We assume that all variables, except V , change with time, and neglect any exchange of inorganic carbon with the atmosphere (as its stock is very small) and any deep-ocean supply of organic carbon.

In the above equations the R and P terms exchange organic and inorganic carbon forms within the upper ocean. In the previous section we argued that the upper-ocean MR is related to community respiration. We may hence envisage that a rapid increase in MR would correspond to an enhancement in total remineralisation, R , made possible thanks to the utilisation of stored organic carbon, i.e. we expect $R > P$. The opposite situation would occur for a rapid decrease in MR, with $P > R$. These transient states contrast with the steady-state condition. The latter corresponds to net carbon loss to the deep ocean being compensated via recirculation of the inorganic carbon and nutrient-rich deep-waters to the surface layers, i.e. the combined expression of the steady-state form of Equations (1) and (2) gives $Q(c + c_d) = Qc_d$. The steady-state net supply of inorganic carbon (and nutrients!) to the upper ocean causes $P > R$; according to Equation (1) the greater the deep concentration reaching the upper ocean, the larger the $P - R$ difference. The long-term mean state, after averaging over one or many full glacial-interglacial cycle, will be $P > R$.

The simplest way to deal with the R and P terms in the above equations is to assume that they combine with the deep-ocean supply to support the change in the system's metabolic state, retrieving/incorporating inorganic carbon (energy) from/into the upper ocean according to the metabolic requirements (as any optimised system would do). The steady-state form of equation (1) actually shows that $R - P + Qc_d$ will eventually reach some value Qc , which is expected to be different for each metabolic state. An initial increase in remineralisation would progressively be replaced by the enhancement of deep supply, in exact analogy to a mammal that begins a high-power activity, initially using reserve ATP until there is sufficient production of aerobic ATP. Hence, we rewrite Equation (1) as

$$\tau \frac{dc}{dt} = \frac{S}{Q} - c, \quad (3)$$

where $S \equiv R - P + Qc_d$ is the energy supply to sustain the change in MR, in units of inorganic carbon per unit time, and $\tau \equiv V/Q$ is an advective time scale, and we have assumed that the upper ocean has a constant volume V .

Let the energy supply be proportional to Q , i.e. $S = Q(t)\gamma(t)$. The steady-state form of Equation (3), $S = Qc$, illustrates that the proportionality function γ sets the concentration level that the system strives

to reach, to be attained if supply remains constant for a sufficiently long time. This value may be as large as the deep-ocean concentration, so that $P = R$, but typically we expect it to be somewhat lower, the difference setting the autotrophic level of the final system, i.e. $P - R = Q(c_d - \gamma)$. The actual difference $c_d - \gamma$ clearly depends on possible changes in the deep-ocean concentrations and the pathways used for deep waters to reach the upper ocean.

Equation (3) may be rewritten as

$$\tau \frac{dc}{dt} = \gamma - c. \quad (3a)$$

A great advantage of this equation is its simplicity, as it only depends on the specified concentration level γ and the advective time scale τ . Let this concentration level be step-like, $\gamma = c_0 + c_1$ during $[t_0, t_1]$ and $\gamma = c_0$ otherwise, and let the overturning rate be given by $Q(t) = Q_0\sigma(t)$, where $\sigma(t)$ is a function to be specified. Under these conditions we may rewrite Equation (3a) as an expression for DIC excess concentration, $\chi \equiv c - c_0$,

$$\tau \frac{d\chi}{dt} = \delta c_1 - \chi, \quad (4)$$

where $\tau \equiv \tau_0/\sigma$, with $\tau_0 = V/Q_0$, and δ is a step function equal to one during $[t_0, t_1]$ and to zero otherwise. The trivial steady-state initial condition is $\chi \equiv 0$ and $Q = Q_0$. The solution is $\chi = c_1[1 - \exp(-E_1/\tau_0)]$ during $[t_0, t_1]$ and $\chi = \chi(t_1) \exp(-E_2/\tau)$ afterwards,

$$\text{where } E_1 \equiv \int_{t_0}^t \sigma dt \text{ and } E_2 \equiv \int_t^{t_1} \sigma dt.$$

The simplest possibility consists in maintaining a constant rate of deep-water formation, $\sigma = 1$. The corresponding increase in inorganic-carbon supply is a step function and the simple solution is $\chi = c_1[1 - \exp(-(t - t_0)/\tau_0)]$ during the step and $\chi = \chi(t_1) \exp(-(t - t_1)/\tau_0)$ after the step. Let us consider an upper ocean of constant depth (about 1300 m, the ocean's area $0.36 \times 10^{15} \text{ m}^2$), and look at the solution for overturning water fluxes $Q = 1.5$ and 3.0 Sv , which correspond to circulation times $\tau_0 = 10$ and 5 ka , respectively (Fig. 6b). Such constant recirculation times cause the upper ocean to display equal (exponential) rates of DIC change after either an increase or a decrease in inorganic-carbon supply; a different τ_0 would not alter this symmetry. The modelled pattern for the DIC excess-concentration is clearly different from the atmospheric CO_2 observations, which display a rapid rise during an

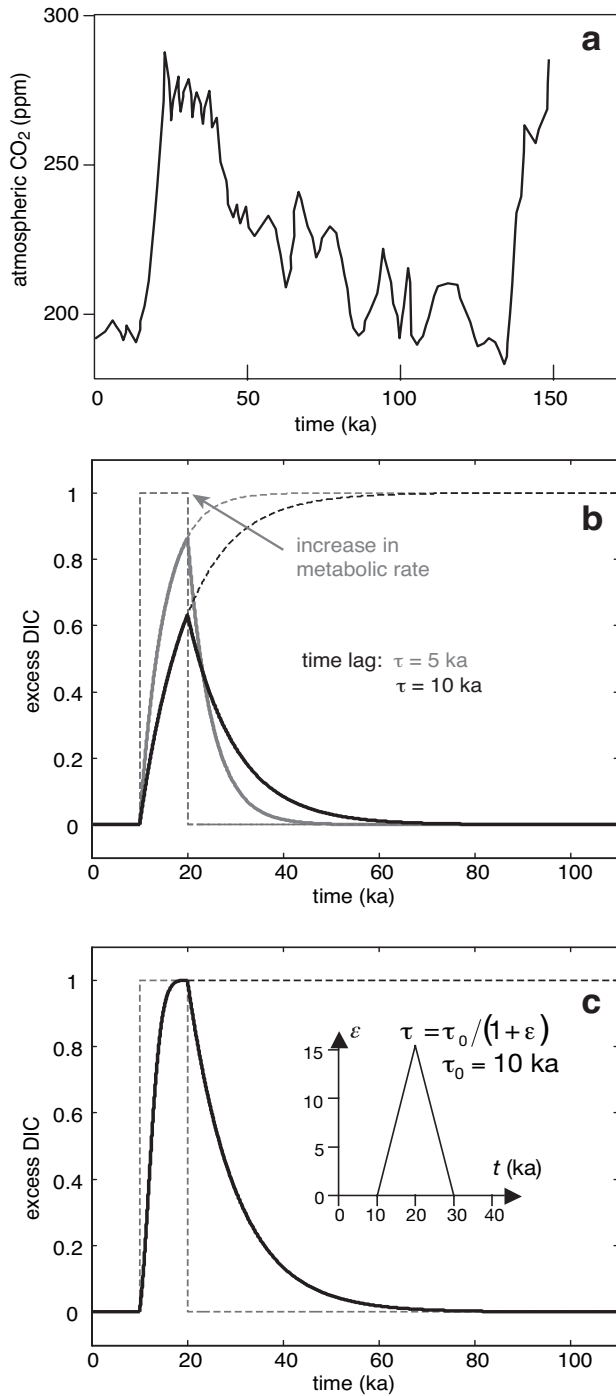


FIG. 6. – (a) Atmospheric CO₂ changes during the last 150 ka, as deduced from the Vostok ice cores from Antarctica, illustrating the rapid increase during interglacial periods followed by a slow decrease during the subsequent glacial period. Adapted from Petit *et al.* (1999). Panels (b) and (c) show the model prediction for changes in DIC in a constant-volume upper ocean (depth about 1300 m) as a result of a step-like increase in the forcing concentration from c_0 to $(c_0 + c_1)$ during $[t_0 = 10 \text{ ka}, t_1 = 20 \text{ ka}]$. The c_1 value is normalised to one. (b) Solution for constant systemic recirculation rates, $Q_0 = 1.5$ and 3.0 Sv , that correspond to advective times $\tau_0 = 10$ and 5 ka , respectively. (c) Solution for a non-constant recirculation rate $Q_0(1 + \epsilon)$, with $Q_0 = 1.5 \text{ Sv}$ ($\tau_0 = 10 \text{ ka}$) and $\epsilon(t)$ increasing linearly from 0 to 15 during $[t_0 = 10 \text{ ka}, t_1 = 20 \text{ ka}]$, and then decreasing at the same rate during $[t_1 = 20 \text{ ka}, t_2 = 30 \text{ ka}]$.

interglacial period but a slow decrease during the subsequent glacial period (Fig. 6a). Further, a constant overturning rate (systemic SV) implies that the inorganic-carbon supply may increase only through the upper-ocean a-v DIC, i.e. by a relatively small $(c_0 + c_1)/c_0$ factor. Thus, the selection of a constant rate $\tau = \tau_0$ does not seem to be a good option.

An illuminating, and yet simple, case corresponds to a rate of deep-water formation of the form $\sigma(t) = (1 + \epsilon(t))$, with $\epsilon(t)$ changing linearly with time. Let us use again the 1300 m constant-depth upper ocean. For this case we consider 1.5 Sv of deep-water formed by the end of the glacial period, increasing linearly to a maximum of 24 Sv by the end of the interglacial period (in 10 ka), and then decreasing back linearly to 1.5 Sv (in another 10 ka) and remaining at this rate until the next interglacial rise. These changes roughly agree with observations of fast/slow deep recirculation during interglacial/glacial ages (Imbrie *et al.*, 1992; Sigman and Boyle, 2000; Sigman and Haug, 2003). This scenario is simulated with $\tau_0 = 10 \text{ ka}$ and $\epsilon(t)$ increasing linearly from 0 to 15 (τ decreasing from 10 ka to 667 yrs) between times $t_0 = 10 \text{ ka}$ and $t_1 = 20 \text{ ka}$, and then diminishing at the same rate (inset in Fig. 6c). In this case the inorganic-carbon supply changes through both the overturning rate and the upper-ocean a-v DIC, in our example the maximum value being a factor $16(c_0 + c_1)/c_0$, one order of magnitude greater than its rest value. During the enhanced metabolic-state the surface concentration rapidly increases up to a constant value imposed by the high-energy requirements, and afterwards it diminishes slowly towards a value that satisfies the low-energy state (Fig. 6c). The predicted upper-ocean DIC, which sets the atmospheric CO₂ fluctuations, nicely reproduces the observed atmospheric CO₂ glacial-interglacial pattern (Petit *et al.*, 1999; Siegenthaler *et al.*, 2005).

We may consider whether our simple model suits observations and box models that predict a decrease in the DIC isotope ratio ¹³C/¹²C during glacial periods (Curry *et al.*, 1988; Toggweiler, 1999). Carbon in organic matter is deficient in ¹³C, so a glacial decrease in this isotope implies a higher organic carbon concentration in the upper ocean and more export to the deep ocean. Combining the steady-state form of Equations (1) and (2) gives $c_r = c_d - c = (c_d - c_0) - \chi$, so in the upper ocean the organic and inorganic carbon concentrations have opposite trends. As the DIC anomaly becomes maximum/minimum during interglacial/glacial peaks (Fig. 6c), this ar-

gument suggests that organic carbon should attain minimum/maximum values, in agreement with some observations. These changes are the system's internal response (remineralisation) to the inorganic carbon deficit/debt during the exercise/recovery phases of the ocean.

A PHYSIOLOGICAL APPROACH TO THE EARTH'S CLIMATE

We have explored the hypothesis that the autotrophic Earth has optimal-organisation pulsating patterns that are self-regulated as for any living being, and that these may be described using macroscopic physiological variables. In the slow-deep (systemic) branch the water parcels replenish their inorganic carbon and nutrient load, while the fast-upper (pulmonary) branch holds a very efficient primary-production system. The pulmonary branch is almost self-sustained as biomass is remineralised to maintain productivity, which produces oxygen and supports its own respiration. This circuit, however, experiences some nutrient and carbon losses that are compensated mainly via equatorial upwelling of the systemic branch. Carbon supply to the euphotic zone occurs very efficiently through the atmosphere, the atmospheric CO₂ being a globally averaged measure of the dissolved inorganic carbon (DIC) difference between outgassing (mainly equatorial upwelling) and ingassing (eutrophic and cold) regions, an index of the arterial-venous differences (a-v DIC) of this primary production organ.

The Earth's pump rate (HR) is the result of seasonal forcing at the ocean surface, i.e. one beat per year. Hence, deep inorganic carbon supply is simply given as the product of the rate of deep-water formation (the systemic stroke volume SV) and the DIC difference between deep upwelled and surface deep-convected waters, a-v DIC. The upper-ocean metabolic rate (MR, in units of inorganic carbon per time) is the energy used by the upper-ocean community to sustain itself, or the difference between gross primary production (PP) and net community production (NCP). The changes in metabolic state are also externally triggered, during the last ca. 800 ka by the 100 ka Milankovitch eccentricity cycle that modulates the amplitude of seasonal insolation (the ocean's action potential). This metabolic pacemaker of the Earth has high impedance, as for all living beings, in the sense that the energy required to modify

the metabolism is very small as compared with the metabolic change itself.

We hypothesise that the Earth system switches between two metabolic states, which correspond to the glacial and interglacial stages, as a result of changes in the seasonal insolation contrast at middle and high latitudes. Although the annual-global mean solar radiation is nearly constant, each state is characterised by quite different overturning rates, so the solar energy incorporated and transformed by the system (external energy) is much greater during interglacial than glacial states. This probably causes interglacial states to be also characterised by the photosynthetic transformation of a much greater fraction of the absorbed solar energy (internal energy). We propose that an increase in internal energy requirements (measured as inorganic nutrients and carbon) is initially supported through enhanced regeneration of inorganic carbon and nutrients, and a steady state is reached only when the inorganic fluxes from the deep ocean can meet the high metabolic expenditure. A decrease in the energetic demand has the opposite effect, with deep carbon and nutrient supply initially exceeding the requirements. The delivery of inorganic carbon and nutrients to the upper ocean, and the transformation between their organic and inorganic forms, has a clear parallelism with the aerobic production of energy and the utilisation or accumulation of anaerobic energy.

These ideas are used to construct an idealised energetic model whose solution, for simple but realistic forcing, produces asymmetric patterns of carbon increase/decrease in the upper ocean that reproduce the glacial atmospheric CO₂ cycles (Petit *et al.*, 1999; Siegenthaler *et al.*, 2005). The interglacial-glacial stages may hence be interpreted as periods of exercise-recovery in the ocean system (Figs. 1 and 6). This explanation opposes the conventional view that the decrease in glacial atmospheric CO₂ is the natural response to increased biological productivity. However, it is coherent with observations that the ocean may currently be heterotrophic (Del Giorgio and Duarte, 2002), with observations of changes in the ¹³C isotope concentration between glacial and interglacial glacial periods (Curry *et al.*, 1988), and with some evidence of decreased productivity during the last glaciation (for a review see Sigman and Haug, 2003). An aspect yet to be elucidated is the relevance of glacial-interglacial changes in deep-ocean nutrient and DIC (Sigman and Haug, 2003), as they must have certainly modulated the above picture.

This work shows that natural climate changes may be studied through a physiological perspective. Such global description could perhaps be considered as a weakness, as it does not explore specific mechanisms, but we interpret it as a strength as it diagnoses the system's macroscopic processes and behaviours, i.e. rather than looking at fluxes it assesses the Earth's heat, carbon, and nutrient balances. There certainly must be many other Earth homeostatic processes that could have physiological equivalents, such as the control of the ocean's pH through the carbon buffering effect (e.g. pH stability in mammal's blood) and the regulation of the ocean's salt content by marginal seas and its effect on the intensity of ocean circulation (e.g. kidney's salt-regulating role in mammals).

Our analysis suggests that during the last ca. 800 ka the ocean's MR has changed between single basal and enhanced states. But, in analogy to many species, whose MR depends on life stage and environmental characteristics, we anticipate that the ocean rate was quite different in earlier geological times, with ice coverage and ocean basins very distant from the present ones. This may have been the case in the late Pliocene, with a dominating 41 ka glacial cycle and a substantially different range in the oxygen isotope record. And, most important to mankind, the ocean's MR may change in the future as a result of human activities. This work proposes that the very much needed prediction of the anthropogenic effect on climate could benefit from a physiological approach.

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REFERENCES

- Antonov, J.I., S. Levitus and T.P. Boyer. – 2004. Climatological annual cycle of ocean heat content. *Geophys. Res. Lett.*, 31: L04304, doi:10.1029/2003GL018851.
- Bejan, A. – 1997. Theory of organization in Nature: pulsating physiological processes. *Int. J. Heat Mass Transfer*, 40: 2097-2104.
- Berger, A.L. – 1978. Long-term variations of daily insolation and Quaternary climatic changes. *J. Atmos. Sci.*, 35: 2362-2367.
- Broecker, W.S., S.L. Peacock, S. Walker, R. Weiss, E. Fahrback, M. Schroeder, V. Mikolajewicz, C. Heinze, R. Key, T.H. Peng and S. Rubin. – 1998. How much deep water is formed in the southern ocean? *J. Geophys. Res.*, 103: 15833-15843.
- Calder, N. – 1974. Arithmetic of ice ages. *Nature*, 252: 216-218.
- Campbell, N.E. – 1990. *Biology*, 2nd ed., Benjamin/Cummings Publishing Company, Redwood City.
- Charlson, R.J., J.E. Lovelock, M.O. Andreae and S.G. Warren. – 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature*, 326: 655-661.
- Conkright, M., S. Levitus and T. Boyer. – 1994. *The World Ocean Atlas 1994, vol 1: Nutrients*, 16 pp., NOAA Atlas NESDIS1, Washington DC.
- Csanady, G.T. – 2001. *Air-sea interaction. Laws and mechanisms*, Cambridge University Press, Cambridge.
- Curry, W.B., J.C. Duplessy, L.D. Labeyrie and N.J. Shackleton. – 1988. Changes in the distribution of $\delta^{13}\text{C}$ of deep water TCO₂ between the last glaciation and the Holocene. *Paleoceanography*, 3: 317-342.
- Del Giorgio, P. and C.M. Duarte. – 2002. Respiration in the open ocean. *Nature*, 420: 379-384.
- Ganachaud, A. and C. Wunsch. – 2000. Improved estimates of global ocean circulation, heat transport and mixing from hydrographic data. *Nature*, 408: 453-457.
- Gill, A. E. – 1982. *Atmosphere-Ocean Dynamics*, Academic Press, New York.
- González-Alonso, J., M.K. Dalsgaard, T. Osada, S. Volianitis, E.A. Dawson, C.C. Yoshiga and N.H. Secher. – 2004. Brain and central haemodynamics and oxygenation during maximal exercise in humans. *J. Physiol.*, 557: 331-342.
- Gouriou, Y. and G. Reverdin. – 1992. Isopycnal and diapycnal circulation of the upper equatorial Atlantic Ocean in 1983-1984. *J. Geophys. Res.*, 97: 3543-3572.
- Guyton A.C. and J.E. Hall. – 2005. *Textbook of medical physiology*, W. B. Saunders Company, Philadelphia.
- Haken, H. – 1983. *Synergetics: An Introduction. Non-equilibrium phase transitions and self-organization in Physics, Chemistry, and Biology*, Springer-Verlag, Berlin.

- Hays, J.D., J. Imbrie and N.J. Shackleton. – 1976. Variations in the Earth's orbit: Pacemaker of the ice ages. *Science*, 194: 1121-1132.
- Ide, K., I.K. Schmalbruch, B. Quistorff, A. Horn and N.H. Secher. – 2000. Lactate, glucose and O₂ uptake in human brain during recovery from maximal exercise. *J. Physiol.*, 522: 159-164.
- Imbrie, J. and J.Z. Imbrie. – 1980. Modelling the climatic response to orbital variations. *Science*, 297: 943-953.
- Imbrie, J., E.A. Boyle, S.C. Clemens, A. Duffy, W.R. Howard, G. Kukla, J. Kutzbach, D.G. Martinson, A. McIntyre, A.C. Mix, B. Molfino, J.J. Morley, L.C. Peterson, N.G. Pisias, W.L. Prell, M.E. Raymo, N.J. Shackleton and J.R. Toggweiler. – 1992. On the structure and origin of major glaciation cycles, 1. Linear responses to Milankovitch forcing. *Paleoceanography*, 7: 701-738.
- Kawase, M. and J.L. Sarmiento. – 1985. Nutrients in the Atlantic thermocline. *J. Geophys. Res.*, 90: 8961-8979.
- La Ferla, R., F. Azzaro, M. Azzaro, G. Caruso, F. Decembrini, M. Leonardi, G. Maimone, L.S. Monticelli, F. Raffa, C. Santinell, R. Zacccone and M.R. d'Alcalá. – 2005. Microbial contribution to carbon geochemistry in the Central Mediterranean Sea: Variability of activities and biomass. *J. Marine Syst.*, 57: 146-166.
- Labeysie, L.D., J.C. Duplessy, J. Duprat, A. Juillet-Leclerc, J. Moyes, E. Michel, N. Kallel and N.J. Shackleton, 1992. Changes in the vertical structure of the North Atlantic Ocean between glacial and modern times. *Quat. Sci. Rev.*, 11: 401-413.
- Louanchi, F. and R.G. Najjar. – 2000. A global monthly climatology of phosphate, nitrate, and silicate in the upper ocean: Spring-summer export production and shallow remineralization. *Global Biogeochem. Cycles*, 14: 957-977.
- Lovelock, J.E. – 1972. Gaia as seen through the atmosphere. *Atmospheric Environ.*, 6: 579-580.
- Lovelock, J.E. and L. Margulis. – 1974. Atmospheric homeostasis by and for the biosphere: the Gaia hypothesis. *Tellus*, 26: 2-10.
- Lozier, M.S., W.B. Owens and R.G. Curry. – 1995. The climatology of the North Atlantic. *Prog. Oceanogr.*, 36: 1-44.
- MacDonald, A.M. and C. Wunsch. – 1996. An estimate of global ocean circulation and heat fluxes. *Nature*, 382: 436-439.
- Margalef, R. – 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, 1: 493-509.
- Margulis, L. and J.E. Lovelock. – 1974. Biological Modulation of the Earth's Atmosphere. *Icarus*, 21: 471-489.
- Najjar, R.G. and R.F. Keeling. – 2000. Mean annual cycle of the air-sea oxygen flux: A global review. *Global Biogeochem. Cycles*, 14: 573-584.
- Nicolis, C. – 1982. Stochastic aspects of climatic transitions – Response to periodic forcing. *Tellus*, 34: 1-9.
- Oort, A.H. and J.P. Peixoto. – 1994. Estimates of the energy cycle of the oceans. *J. Geophys. Res.*, 99: 7665-7688.
- Orsi, A.H., G.H. Johnson, and J.L. Bullister. – 1999. Circulation, mixing and production of Antarctic bottom water. *Prog. Oceanogr.*, 43: 55-109.
- Paillard, D. – 1998. The timing of Pleistocene glaciations from a simple multiple-state climate model. *Nature*, 391: 378-381.
- Paillard, D. and F. Parrenin. – 2004. The Antarctic ice sheet and the triggering of deglaciations. *Earth Planet. Sci. Lett.*, 227: 263-271.
- Pelegri, J.L. and G.T. Csanady. – 1991. Nutrient transport and mixing in the Gulf Stream. *J. Geophys. Res.*, 96: 2577-2583.
- Pelegri, J.L., G.T. Csanady and A. Martins. – 1996. The North Atlantic nutrient stream. *J. Oceanogr.*, 52: 275-299.
- Pelegri, J.L., A. Marrero-Díaz and A.W. Ratsimandresy. – 2006. Nutrient irrigation of the North Atlantic. *Prog. Oceanogr.*, 70: 366-406.
- Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V.M. Kotlyakov, M. Legrand, V.Y. Lipenkov, C. Lorius, L. Pépin, C. Ritz, E. Saltzman, and M. Stievenard. – 1999. Climate and atmospheric history of the past 420000 years from the Vostok ice core, Antarctica. *Nature*, 399: 429-436.
- Platt, T., W.G. Harrison, M.R. Lewis, W.K.W. Li, S. Sathyendranath, R.E. Smith and A.F. Vezina. – 1989. Biological production of the oceans: the case for consensus. *Mar. Ecol. Prog. Ser.*, 52: 77-88.
- Pomeroy, L.R., W.J. Wiebe, D. Deibel, R.J. Thompson and G.T. Rowe. – 1991. Bacterial responses to temperature and substrate concentration during the Newfoundland spring bloom. *Mar. Ecol. Prog. Ser.*, 75: 143-159.
- Randall, D., W. Burggren and K. French. – 2002. *Eckert animal physiology: Mechanisms and adaptations*, W.H. Freeman and Company, New York.
- Raymo, M.E. – 1997. The timing of major climate terminations. *Paleoceanography*, 12: 577-585.
- Raymo, M.E. and K. Nisancioglu. – 2003. The 41 kyr world: Milankovitch's other unsolved mystery. *Paleoceanography*, 18: Art. No. 1011, doi:10.1029/2002PA000791.
- Reid, J.L. – 1994. On the total geostrophic circulation of the North Atlantic Ocean: flow patterns, tracers, and transports. *Prog. Oceanogr.*, 33: 1-92.
- Ridgwell A.J., A.J. Watson and M.E. Raymo. – 1999. Is the spectral signature of the 100 kyr cycle consistent with a Milankovitch origin? *Paleoceanography*, 4: 437-440.
- Rintoul, S.R. and C. Wunsch. – 1991. Mass, heat, oxygen and nutrient fluxes and budgets in the North Atlantic Ocean. *Deep-Sea Res.*, 38 (S1): S355-S377.
- Rivkin, R.B. and L. Legendre. – 2001. Biogenic carbon cycling in the upper ocean: Effects of microbial respiration. *Science*, 291: 2398-2400.
- Saenko, O., A. Weaver and M.H. England. – 2003. A region of enhanced northward Antarctic Intermediate Water transport in a coupled climate model. *J. Phys. Oceanogr.*, 33: 1528-1535.
- Sarmiento, J.L., N. Gruber, M.A. Brzezinski and J.P. Dunne. – 2003. High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature*, 427: 56-60.
- Schmitz, W.J. – 1995. On the interbasin-scale thermohaline circulation. *Rev. Geophys.*, 33: 151-173.
- Shackleton, N.J. – 2000. The 100000-year ice-age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. *Science*, 289: 1897-1902.
- Siegenthaler, U., T.F. Stocker, E. Monnin, D. Lüthi, J. Schwander, B. Stauffer, D. Raynaud, J.M. Barnola, H. Fischer, V. Masson-Delmotte and J. Jouzel. – 2005. Stable carbon-climate relationship during the late Pliocene. *Science*, 310: 1313-1317.
- Sigman, D.M. and E.A. Boyle. – 2000. Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, 407: 859-869.
- Sigman, D.M. and G.H. Haug. – 2003. The biological pump in the past. In: D. Holand and K.K. Turekian (eds.), *Treatise on Geochemistry*, vol 6, pp. 491-528, Elsevier, London.
- Signorini, S. R., R.G. Murtugudde, C.R. McClain, J.R. Christian, J. Picaut and A.J. Busalacchi. – 1999. Biological and physical signatures in the tropical and subtropical Atlantic. *J. Geophys. Res.*, 104: 18367-18382.
- Stommel, H. – 1979. Determination of water mass properties of water pumped down from the Ekman layer to the geostrophic flow below. *Proc. Natl. Acad. Sci. USA*, 76: 3051-3055.
- Sundquist, E.T. and K. Visser. – 2003. The geological history of the carbon cycle. In: D. Holand and K.K. Turekian (eds.), *Treatise on Geochemistry*, vol 6, pp. 425-472, Elsevier, London.
- Takahashi, T., S.C. Sutherland, C. Sweeney, A. Poisson, N. Metz, B. Tilbrook, N. Bates, R. Wanninkhof, R.A. Feely, C. Sabine, J. Olafsson and Y. Nojiri. – 2002. Global sea-air CO₂ flux based on climatological surface ocean pCO₂, and seasonal biological and temperature effects. *Deep-Sea Res. II*, 49: 1601-1622.
- Talley, L.D., J.L. Reid and P.E. Robbins. – 2003. Data-based meridional overturning streamfunctions for the global ocean. *J. Climate*, 16: 3213-3226.
- Toggweiler, J.R. – 1999. Variation of atmospheric CO₂ by ventilation of the ocean's deepest water. *Paleoceanography*, 14: 571-588.
- Watson, A.J. and J.E. Lovelock. – 1983. Biological homeostasis of the global environment: the parable of Daisyworld. *Tellus*, 35B: 284-289.
- Williams, M., D. Dunkerley, P. de Deckker, P. Kershaw and J. Chappell. – 1998. The Milankovitch hypothesis and quaternary environments. In: M. Williams, D. Dunkerley, P. de Deckker, P. Kershaw, and J. Chappell (eds.), *Quaternary Environments*, pp. 73-106, Arnold Publishers, London.
- Williams, R.G. and M.J. Follows. – 2003. Physical transport of nutrients and the maintenance of biological production. In: M. Fasham (ed.), *Ocean Biogeochemistry: the role of the ocean carbon cycle in global change*, pp. 19-51, Springer, New York.
- Williams, R.G., V. Roussinov and M.J. Follows. – 2006. Nutrient streams and their induction into the mixed layer. *Global Biogeochem. Cycles*, 20: GB1016, doi:10.1029/2005GB002586.

Wunsch, C. and R. Ferrari. – 2004. Vertical mixing, energy, and the general circulation of the oceans. *Ann. Rev. Fluid Mech.*, 36: 281-314.

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