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Nutrient Cycling in the Mediterranean Sea: The Key to Understanding How the Unique Marine Ecosystem Functions and Responds to Anthropogenic Pressures¹

Helen R. Powley, Philippe Van Cappellen and Michael D. Krom

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Abstract

The Mediterranean Sea is a marine desert: although it receives large nutrient inputs from a rapidly growing coastal population, its offshore waters exhibit extremely low biological productivity. Here, we use a mass balance modelling approach to analyse the sources and fate of the two main nutrients that support marine biomass production: phosphorus (P) and nitrogen (N). Surprisingly, the main source of P and N to the Mediterranean Sea is North Atlantic surface water entering through the Strait of Gibraltar, not emissions from surrounding land. The low biological productivity of the Mediterranean Sea is linked to the switch from less bioavailable nutrients entering the basin to highly bioavailable nutrients leaving it although similar amounts of total P and N enter and leave the Mediterranean Sea. This unique feature is a direct consequence of its unusual anti-estuarine circulation. An important environmental implication of the anti-estuarine circulation is that it efficiently removes excess anthropogenic nutrients entering the Mediterranean Sea, thus protecting offshore waters against eutrophication contrary to other semi-enclosed marine basins. In a similar vein, the “self-cleaning” nature of the Mediterranean Sea may prevent severe oxygen depletion of Mediterranean deep waters should ongoing climate warming lead to a weakening of the thermohaline circulation.

Keywords: Mediterranean Sea, nutrients, phosphorus, nitrogen, mass balance modelling, circulation, climate and environmental change, deep-water oxygenation

¹Words or phrases marked for the first time in ***bold italics*** are defined in the glossary.

1. Introduction and background

The Mediterranean Sea (**Figure 1**) has been described as the cradle of western civilization. It is a sea of far greater importance to humanity than would be inferred from its size, as illustrated in the other chapters of this book and elsewhere. In modern times the Mediterranean Sea has become the receptacle of rising nutrient wastes from the surrounding countries. When discharged into coastal waters and inland seas, compounds containing phosphorus (P) and nitrogen (N), two chemical elements collectively known as plant macronutrients, enhance the growth of *phytoplankton*. The synthesis of new biomass by phytoplankton is termed *primary production*. Excessive phytoplankton growth leads to many and varied problems associated with *eutrophication*, including toxic algal blooms, dead *hypoxic* areas and, sometimes, major fish kills. In the Mediterranean Sea, nutrient discharges are causing problems locally, such as in the North Adriatic Sea, Venice Lagoon or lagoons in the Nile Delta. However, unlike other semi-enclosed seas, there is little evidence for increasing primary production in the offshore waters of the Mediterranean Sea. In fact, the vivid blue waters of the Mediterranean Sea reflect the very low biomass of phytoplankton (the ‘grass’ of the world’s oceans) making it as much a desert as the Sahara to the south (**Figure 2**). A key question, which we address in this chapter, is: why does primary production in the Mediterranean Sea remain one of the lowest of the world’s ocean despite the high inputs of excess anthropogenic P and N? It is well known that the primary productivity of marine surface waters is controlled by the supply of macronutrients (i.e. P and N) plus the amount of light. The Mediterranean Sea has abundant sunlight, and the land-derived nutrient supply is similar to that of the Baltic Sea where problems of eutrophication, including nuisance algal blooms, are common. What makes the Mediterranean Sea special?

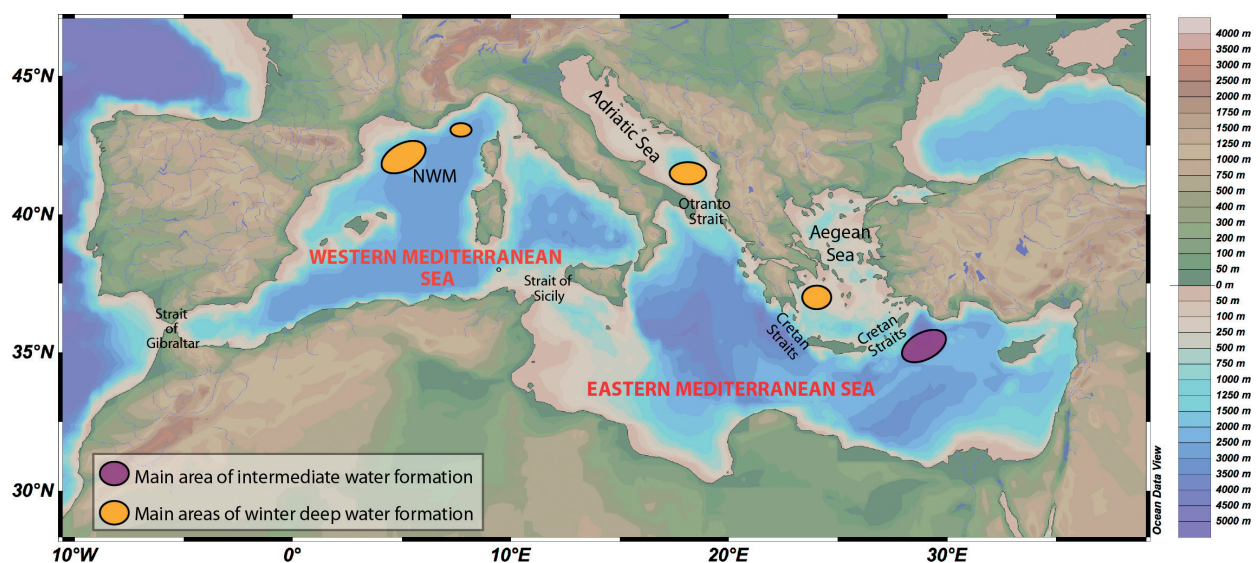


Figure 1. Map of the Mediterranean Sea, including the major areas of formation of intermediate and deep waters. After de Madron et al. [1]. NWM = north-west Mediterranean Sea. This figure is available in colour in the online version of this chapter.

The work presented in this chapter is based on mass balance model calculations that quantitatively describe the sources, fate and transport of the nutrient elements P and N in the Mediterranean Sea. The calculations help explain not only why the Mediterranean Sea is a marine desert but also why the nutrient distributions differ between the Eastern and Western Mediterranean Seas. In addition, we explore how the Mediterranean Sea has responded to the large increases in anthropogenic nutrient inputs since the middle of the last century and whether changes in circulation due to climate change have the potential to lead to a depletion of the dissolved oxygen (O_2) levels in the deep waters of this semi-enclosed marine basin. As far as possible, the text explains briefly the major ocean processes occurring in ways that, hopefully, make the text accessible to readers with a non-expert knowledge of oceanography and marine science.

1.1. The Gaia hypothesis: how marine phytoplankton control their chemical environment

In 1979, James Lovelock in his landmark book *Gaia: A New Look at Life on Earth* advocated a new way of looking at the planetary ecosystem, which he called the Gaia hypothesis. The Gaia hypothesis states that living organisms and nonliving natural compounds are part of a highly coupled, dynamic system that shapes and regulates the earth's environment. It is this interactive system that maintains the Earth as a planet where life as we know it can exist. Lovelock developed his theory when comparing the chemical composition of the atmospheres on Earth and on Mars and asking the question: Why are they so different? In particular, why is there so much free O_2 on Earth and so little on Mars? His answer was that plants produce molecular O_2 , which then accumulates and in turn is essential for all living animals to breathe. Overall, the production and consumption of O_2 closely track each other, hence allowing the atmospheric O_2 level to remain relatively stable over time. When this balance is severely perturbed, atmospheric O_2 may quickly collapse as probably happened on Mars. The Gaia theory has been central to much of the way we look at the mutual interactions between biological processes and their physical and chemical environment. Marine scientists have been looking at



Figure 2. The clear blue waters of the Mediterranean Sea reflect the very low biological productivity of its surface waters compared to most of the world's oceans. Thus, the Mediterranean Sea is as much of a 'desert' as the Sahara Desert to the south (photographs taken by G. Rilov and by N. Landsberg). This figure is available in colour in the online version of this chapter.

the ocean in a similar way for a long time: the so-called Redfield ratio is in effect Gaia as applied to the world's oceans.

What is the Redfield ratio? Look at the chemical equation in **Figure 3**: it represents the synthesis of new biomass by marine phytoplankton. The equation shows that for every 106 carbon (C) atoms that are incorporated in new biomass on average, 16 atoms of N and 1 atom of P are utilized. In 1936, Alfred Redfield, a marine scientist working at Harvard University, noticed that the dissolved nitrate-to-dissolved phosphate ratio in deep ocean waters in many parts of the globe is close to 16:1 (in units of mol/mol) that is the same value as the average N/P ratio of marine phytoplankton. He suggested that this surprising convergence reflects a biological control over the distribution of vital nutrient elements in seawater [2].

Marine phytoplankton produce biomass with an atomic (or molar) N/P ratio of 16:1. After death, the plankton biomass settles as biological debris towards the bottom of the oceans. The degradation of this debris, primarily by microorganisms, then releases the N and P as dissolved nitrate and phosphate to the water column in a 16:1 proportion. Upward mixing and *upwelling* return the dissolved inorganic nutrients to the surface waters where they are used again for primary production, and so the cycling of the N and P continues at the beat of the Redfield ratio. Additional biological processes further balance any departure of the supply of the inorganic nutrients from the required 16:1 ratio. When N is in short supply, *nitrogen fixation* transforms dinitrogen gas (N₂) from the atmosphere into chemical forms that can be used by phytoplankton, while excess dissolved nitrate is removed by the process of *denitrification*. Given sufficient time, the balance between the various processes ultimately drives the nitrate to phosphate ratio of seawater towards the Redfield value of 16:1 [3].

1.2. On the uniqueness of the Mediterranean Sea

One of the unique features of the Mediterranean Sea is that the dissolved P and N concentrations in the water column do NOT obey the Redfield ratio. The dissolved nitrate-to-phosphate ratio of the deep waters is around 23:1 in the Western Mediterranean Sea and 28:1 in the Eastern Mediterranean Sea ([4]; **Figure 4**). Similarly, the ratios of dissolved organic N to dissolved organic P (DON/DOP) and particulate organic N to particulate organic P (PON/

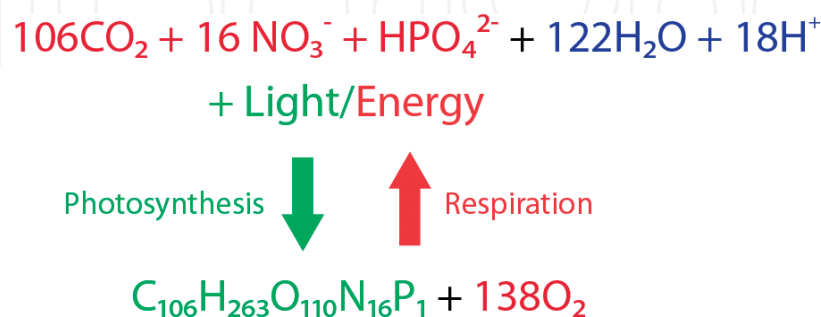


Figure 3. Net reaction showing the utilization of inorganic chemical ingredients by marine phytoplankton as they carry out photosynthesis and produce new biomass. The reverse reaction is respiration in which organisms use organic substrates as food to produce energy. Note that molecular oxygen (O₂) is generated during photosynthesis and consumed during respiration.

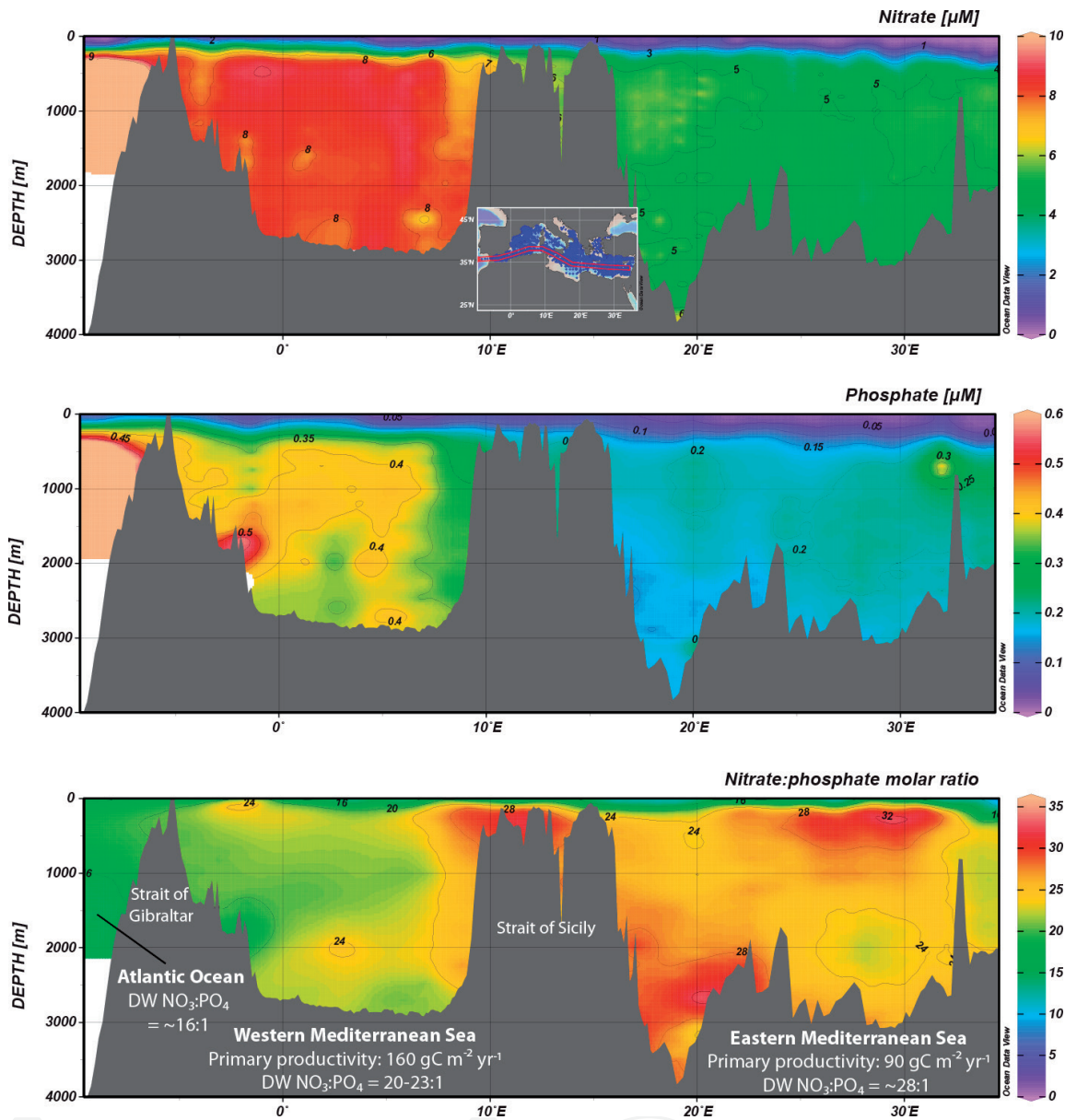


Figure 4. Distributions of dissolved nitrate and phosphate concentrations and the dissolved nitrate to dissolved phosphate molar ratio, in the water column of the North Atlantic Ocean, Western Mediterranean Sea and Eastern Mediterranean Sea. Note the differences in scales between the two uppermost panels. The figures are generated in Ocean Data View [11], using the data in Lavezza et al. [12]. This figure is available in colour in the online version of this chapter.

POP) typically exceed 16:1 in Mediterranean seawater [5–9]. In other words, compared to the world's ocean, the Mediterranean Sea is chronically short of P: it is in fact P-starved. One outcome of this highly unusual situation is that many bacteria and phytoplankton that live in the Mediterranean Sea have adapted to survive under severe P limitation [10].

Phytoplankton biomass in the Mediterranean Sea is also extremely low. A commonly used way to determine the phytoplankton abundance is to measure the amount of chlorophyll, the green pigment that plants use to capture light energy during photosynthesis. Compared with other semi-enclosed seas adjacent to the European continent, such as the Baltic Sea or North

Sea, the summer chlorophyll levels of the Mediterranean Sea are an order of magnitude lower (**Figure 5**). The chlorophyll concentrations in many European and other semi-enclosed seas often reach levels where eutrophication starts having harmful ecological impacts. With the exception of nearshore areas, this is not observed in the Mediterranean Sea.

The low phytoplankton biomass matches the very low primary production observed in the open waters of the Mediterranean Sea: in fact, offshore primary production is one of the lowest observed in the global ocean. Values reported for the Eastern Mediterranean Sea, $10\text{--}143\text{ g C m}^{-2}\text{ y}^{-1}$ ([14]; **Table 1**), are even lower than those in the centre of large *ocean gyres*, such as the Sargasso Sea, where values are around $150\text{ g C m}^{-2}\text{ y}^{-1}$. For comparison, the average primary productivity of the coastal ocean is $350\text{ g C m}^{-2}\text{ y}^{-1}$, while that of upwelling zones, some the most productive areas of the ocean typically exhibit values in excess of $500\text{ g C m}^{-2}\text{ y}^{-1}$. Bodies of water with low primary production are called *oligotrophic*. Examples of oligotrophic systems are ocean gyres and the Western Mediterranean Sea. The Eastern Mediterranean Sea, with a primary productivity that is about three times lower than that of the Western Mediterranean Sea, is referred to as ultra-oligotrophic.

Ultimately, the low biological productivity of the Mediterranean Sea is due to the low availability of inorganic nutrients (in particular, dissolved phosphate, nitrate and ammonia) that are needed for phytoplankton to grow (**Figure 3**). The vertical distributions of dissolved inorganic nutrients in the oceans exhibit the lowest concentrations in the surface waters where

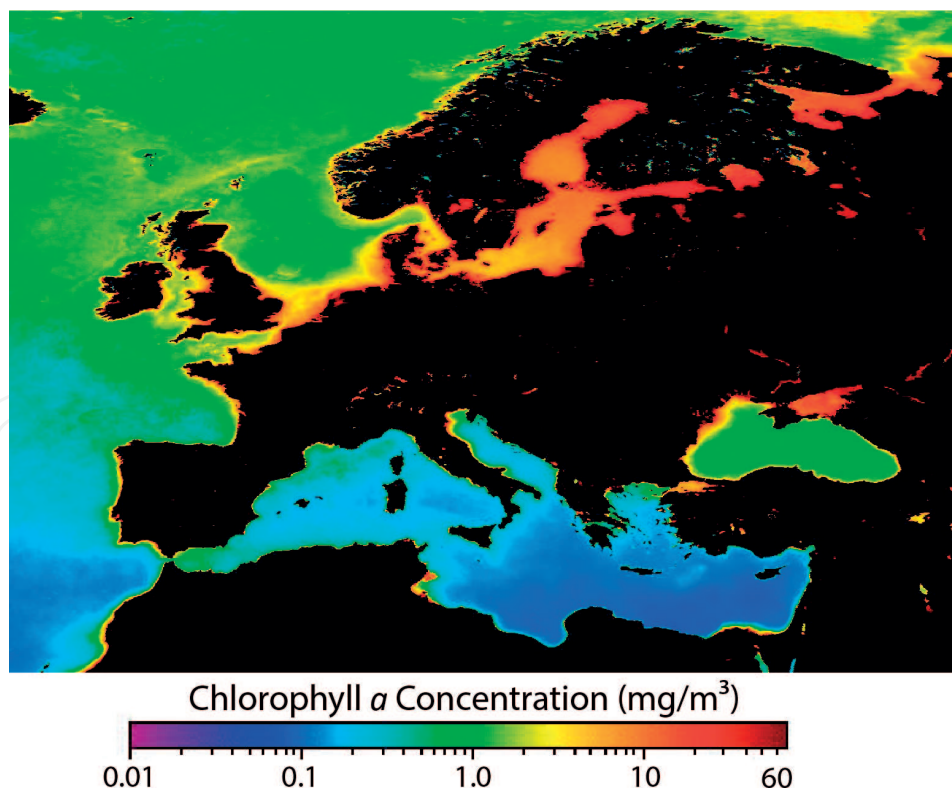


Figure 5. Summer surface water chlorophyll showing low concentrations in the Mediterranean Sea compared to other inland and coastal European waters. The concentrations displayed are average values recorded between July 2002 and December 2004. From NASA [13]. This figure is available in colour in the online version of this chapter.

Area of the ocean	Primary productivity (gC m ⁻² y ⁻¹)	Reference
Eastern Mediterranean Sea	10–143	[14]
Western Mediterranean Sea	37–475	[14]
Open ocean (average)	75	[15]
Continental shelves (average)	300	[15]
Upwelling regions (average)	500	[15]
Primary productivity is expressed in units of mass of carbon fixed in photosynthesis, per unit sea surface area per unit of time.		

Table 1. Average primary productivity in the Eastern and Western Mediterranean Seas compared with average values for the global ocean.

the nutrients are actively taken up by phytoplankton. Below the depth of light penetration, the concentrations of dissolved inorganic P and N increase as they are regenerated by the breakdown of settling biological debris (i.e., *respiration*). This pattern is observed throughout the world's oceans. However, the absolute concentrations of dissolved inorganic P and N in deep-water masses vary substantially from location to location. In the global ocean, the lowest deep-water concentrations of dissolved inorganic P and N are found in the North Atlantic Ocean, where deep water is newly formed by *downwelling* of nutrient-poor surface water. The deep waters subsequently accumulate dissolved inorganic nutrients as they travel through the South Atlantic Ocean and into the Indian Ocean and Southern Pacific Ocean. The highest dissolved inorganic P and N concentrations are therefore at the end of the so-called global conveyor belt in the Northern Pacific (**Table 2**). As can be seen, the concentrations of dissolved inorganic P and N in the waters of the major deep sea basins are systematically higher than those found in the Western Mediterranean Sea, which themselves are higher than those in the Eastern Mediterranean Sea (see also **Figure 4**).

Key to interpreting the unique features of the Mediterranean Sea discussed above is its *anti-estuarine circulation* (**Figure 6**). North Atlantic surface water flows into the Western Mediterranean Sea via the Strait of Gibraltar. This surface water flows east and gets progressively warmer and more saline because of the Mediterranean climate that, particularly in summer, is hot and dry. The modified Atlantic surface water enters the Eastern Mediterranean Sea through the Strait of Sicily and continues to flow eastwards. Eventually, it turns northwards until it reaches the southern coast of Turkey where, during the winter, it cools sufficiently to become denser than the surrounding water, which causes downwelling and formation of new intermediate water. This intermediate water then flows westwards and back out of the Eastern Mediterranean Sea through the Strait of Sicily, eventually reaching the Strait of Gibraltar and returning Mediterranean seawater to the North Atlantic Ocean. Thus, at both straits, the eastward surface inflow is balanced by a deeper, more saline and denser westward outflow. The only other major water body exhibiting a similar anti-estuarine circulation is the Red Sea, which is also very oligotrophic. Most semi-enclosed marine basins (e.g. the Baltic Sea) have an estuarine circulation with surface (less saline) water flowing out into the open ocean and deeper (more saline) seawater flowing land inwards. The implications of

Nutrient	Eastern Mediterranean Sea	Western Mediterranean Sea	North Atlantic Ocean	North-West Pacific Ocean
	$\mu\text{mol l}^{-1}$			
Nitrate	6	9	16	50
Phosphate	0.25	0.4	1	3
Silicic acid	6–12	10–32	20	160

Note that silicic acid, or dissolved silica, is essential to the growth of an important group of phytoplankton called diatoms. The concentration values are given in units of micromoles per litre seawater where micro (μ) stands for 10^{-6} .

Table 2. Typical concentrations of dissolved inorganic nutrients in the deep waters of the Eastern and Western Mediterranean Seas compared with concentrations found in the deep waters of the global ocean.

the anti-estuarine circulation for the biogeochemical processes in the Mediterranean Sea are discussed below.

1.3. Mass balance modelling: nutrient cycling in the Mediterranean Sea

Mass balance models, also called box models, provide a simple but powerful tool to analyse complex environmental systems such as the Mediterranean Sea. These models require relatively little data and have low spatial and temporal resolution, yet they can yield some profound insights into the large-scale dynamics of coupled biogeochemical cycles. The starting point for the Mediterranean nutrient model is to determine how much P and N enter and leave the system. Once we then add our knowledge of the main in-system biogeochemical

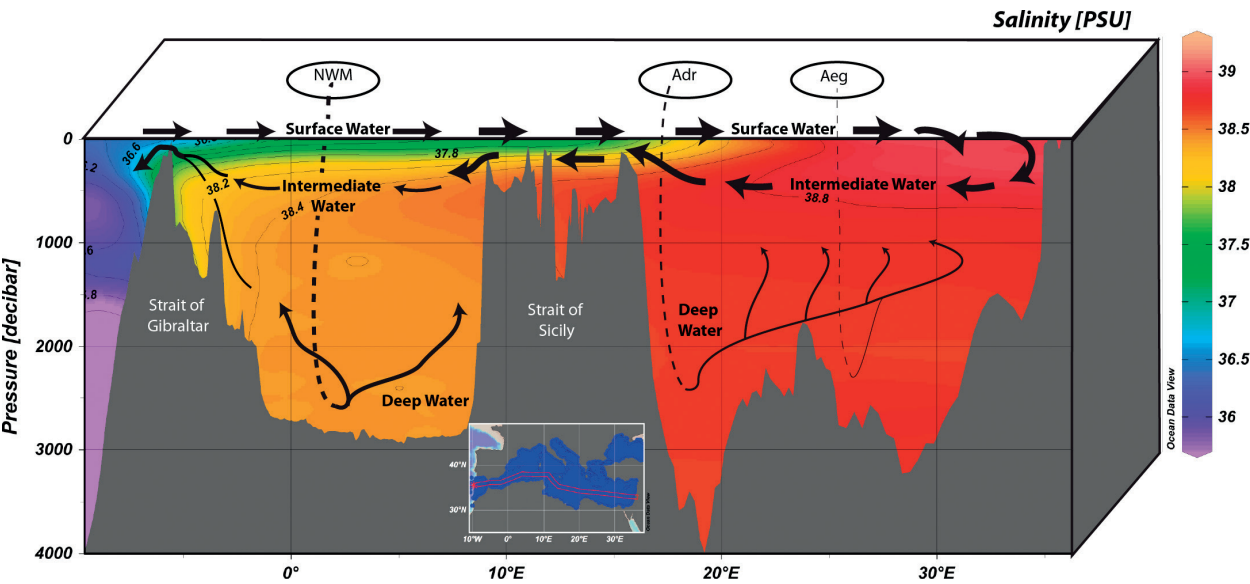


Figure 6. Cross section showing the distribution of salinity (colour) and the general circulation of the Mediterranean Sea (arrows). The thicknesses of the arrows indicate the relative flow rates. Major deep-water formation areas are identified (see also **Figure 1**): NWM = north-west Mediterranean Sea; Adr = Adriatic Sea; Aeg = Aegean Sea. Salinity data from MEDAR Group [16]. Figure generated in Ocean Data View [11]. This figure is available in colour in the online version of this chapter.

processes, it is possible to simulate the general trends of nutrient cycling in the Mediterranean Sea [17] and predict what changes may be expected under the influence of anthropogenic nutrient enrichment and global climate change [18, 19].

In the model, the Western and Eastern Mediterranean Seas are each divided into three layers: surface water, intermediate water and deep water. The water cycle describes the flows between the six water layers, plus the inflow and outflow exchanges with adjacent basins, including the Atlantic Ocean, the Adriatic Sea and the Aegean Sea. Once the water flows are assigned, the nutrient chemistry is added. Both inorganic and organic dissolved forms of P and N are included in the model, as well as particulate organic P and N to represent the nutrients associated with biological material, live and dead. Average concentrations of all the P and N chemical species in the six water layers are derived from measurements made during oceanographic cruises in the Mediterranean Sea. This gives a total of 42 individual chemical P plus N reservoirs or boxes. The transformations of the chemical species from one form to another are represented by dynamic rate expressions. Thus, for example, primary production transforms inorganic dissolved P (phosphate) and N (nitrate) into particulate organic P and N. In the model, the rates at which P and N are used in primary production are coupled to one another by the Redfield ratio.

The P and N model was initialized for conditions corresponding to the year 1950. We chose 1950 because the earliest oceanographic surveys of the Mediterranean Sea date back to the middle of the twentieth century, that is, nutrient time series data are available from that time on. In addition, anthropogenic nutrient inputs from the surrounding countries increased rapidly after 1950, in particular because of the systematic introduction of fertilizers in agriculture. To close the 1950 budgets of P and N, we made a crucial assumption, namely, that all the reservoirs were at steady state in 1950, that is, inputs and outputs to each reservoir were perfectly balanced. The model was then run forwards in time taking into account the temporal changes in P and N inputs due to human activities. The steady-state model simulations for 1950 and the time-dependent post-1950 simulations were used to answer a series of quantitative questions about how the Mediterranean Sea works and why it is such an unusual marine ecosystem.

2. Understanding the unusual properties of the Mediterranean Sea

2.1. Marine-derived P and N inputs exceed those from the surrounding land

A significant result of our analysis is that the main source of P and N to the Mediterranean Sea is the horizontal inflow of surface water from the North Atlantic Ocean through the Strait of Gibraltar (**Figures 7 and 8**). This is unexpected given that the Mediterranean Sea is almost entirely surrounded by land with correspondingly large nutrient emissions from land-based human activities. The reason lies in the large volume of Atlantic water entering the Western Mediterranean Sea driven by the intense anti-estuarine circulation. According to our estimates, inflowing Atlantic surface water (also referred to as ASW) provides 58% of the total P input to the Western Mediterranean Sea (**Figure 7**) and accounts for 39% of its *new production*, that is, the primary production supported by external sources of P to the *photic zone*, rather than supported by recycled nutrients from the degradation of biological materials within the surface

waters. In a similar vein, the inflow of Western Mediterranean surface water through the Strait of Sicily represents 77% of the total P input to the Eastern Mediterranean Sea (**Figure 7**) and supports 37% of its new production. In addition, much of the new production, 26 and 37% in the Western and Eastern Mediterranean Seas, respectively, can be attributed to inputs of DOP.

Interestingly, recent research has shown that horizontal (or lateral) nutrient inputs, and in particular those of DOP and DON, are a major part of the nutrient budgets and new production of subtropical oceanic gyres [20]. This, in some respects, means that the Mediterranean Sea behaves more like a subtropical ocean gyre than other semi-enclosed marine basins. While at first this may be surprising, it starts to make sense when we compare the circulation regimes of oceanic gyres and the Mediterranean Sea. In subtropical gyres the Coriolis force, the force created by the spinning of the Earth, forces surface water towards the centre of the gyre where it is subsequently forced downwards before moving outwards. That is, lateral inflow from outside the gyre leads to downwelling inside the gyre, followed by outflow at greater depth. This is similar to the general flow pattern in the Mediterranean Sea, which is also characterized by lateral surface inflow and deeper lateral outflow (**Figure 6**). Note, however, that the forcing mechanisms, the Coriolis force and the anti-estuarine circulation, are quite different.

2.2. Why is the Mediterranean Sea a biological desert?

The most biologically active forms of P (dissolved phosphate) and N (dissolved nitrate and ammonia) are easily assimilated by phytoplankton that form the base of the food web. Most phytoplankton do not die of 'old age', but are eaten by larger organisms, which in turn are eaten by even larger organisms. Eventually, biological material produced in the surface waters drops out of the photic zone either as the faeces of zooplankton or as part of what is called *marine snow*. The organic matter settles into the intermediate water where much of it is converted back into phosphate and nitrate through *solubilization* and *mineralization*. In addition, some of the dissolved and particulate nutrients present in the surface water are transported down when intermediate water forms in the winter. In contrast with much of the rest of the ocean, very little of the regenerated, and highly bioavailable, dissolved inorganic nutrients in the Mediterranean Sea make it back into the photic zone. There is almost no upwelling of intermediate water to the surface in the Eastern Mediterranean Sea and only some upwelling in the Western Mediterranean Sea. Instead, because of the anti-estuarine circulation, most intermediate water flows out of both the Eastern and Western Mediterranean Seas carrying with it the highly bioavailable nutrients, which are eventually lost to the Atlantic Ocean.

An important finding of the mass balance calculations is that the low productivity of the Mediterranean Sea is not so much caused by a net total loss of nutrients to the Atlantic Ocean, but rather by the differences in chemical forms of P and N entering and leaving the basin. In fact, the inflows of total P and total N to the Mediterranean Sea through the Strait of Gibraltar are of comparable magnitudes as the corresponding outflows of total P and total N with deeper Mediterranean Sea water (**Figures 7 and 8**). However, the P and N exiting the Mediterranean Sea are predominantly in their most biologically active forms, dissolved phosphate and nitrate,

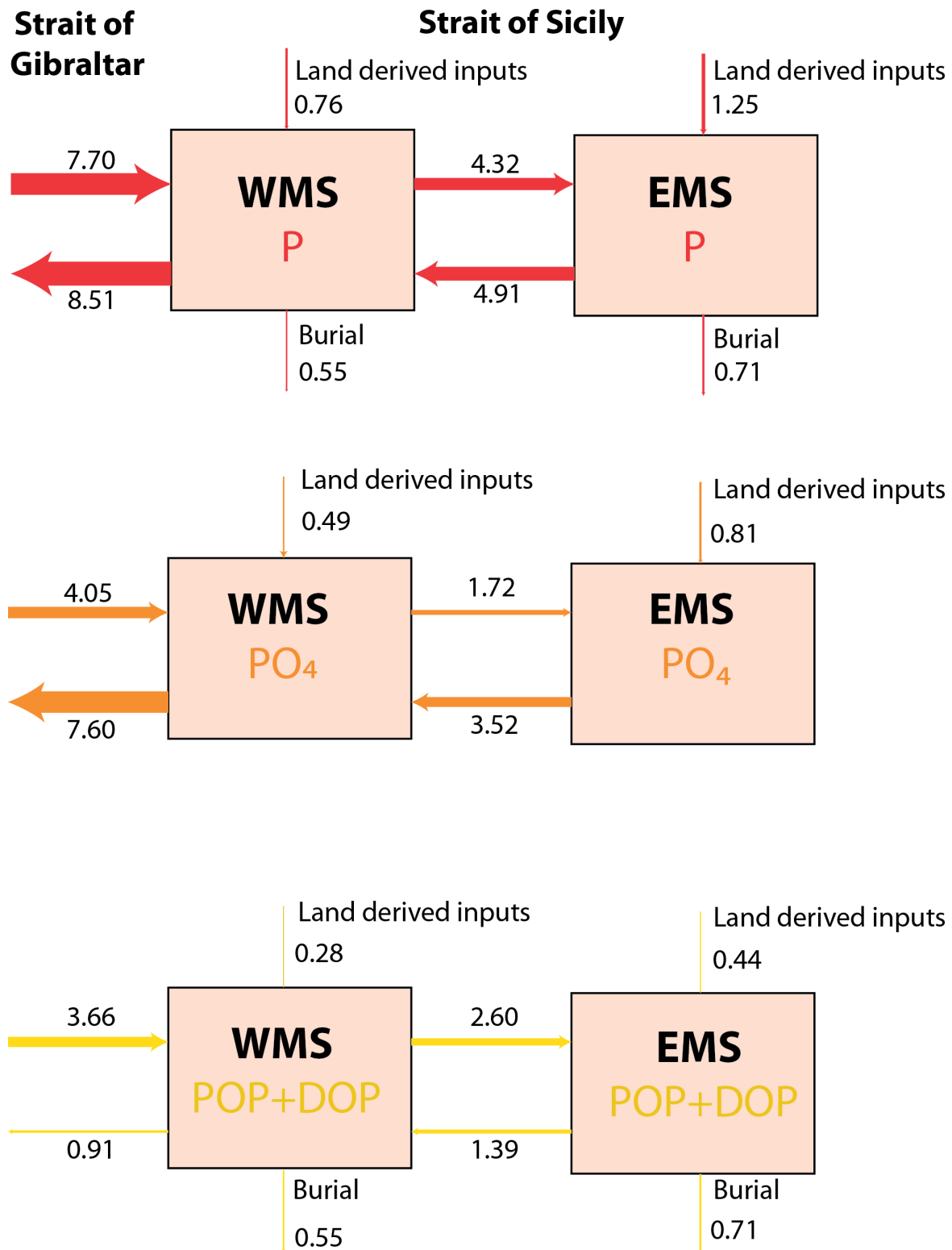


Figure 7. Input and output fluxes of reactive phosphorus (P), dissolved inorganic phosphorus (PO_4) and particulate and dissolved organic phosphorus (POP + DOP) to the Western Mediterranean Sea (WMS) and Eastern Mediterranean Sea (EMS). The thicknesses of the arrows scale to the corresponding fluxes. Numerical values are fluxes in units of $10^9 \text{ mol P y}^{-1}$ [17]. Fluxes can be converted to units of $\text{mol m}^{-2} \text{ y}^{-1}$ by dividing them by the surface areas of the WMS and EMS, $815 \times 10^9 \text{ m}^2$ and $1336 \times 10^9 \text{ m}^2$, respectively.

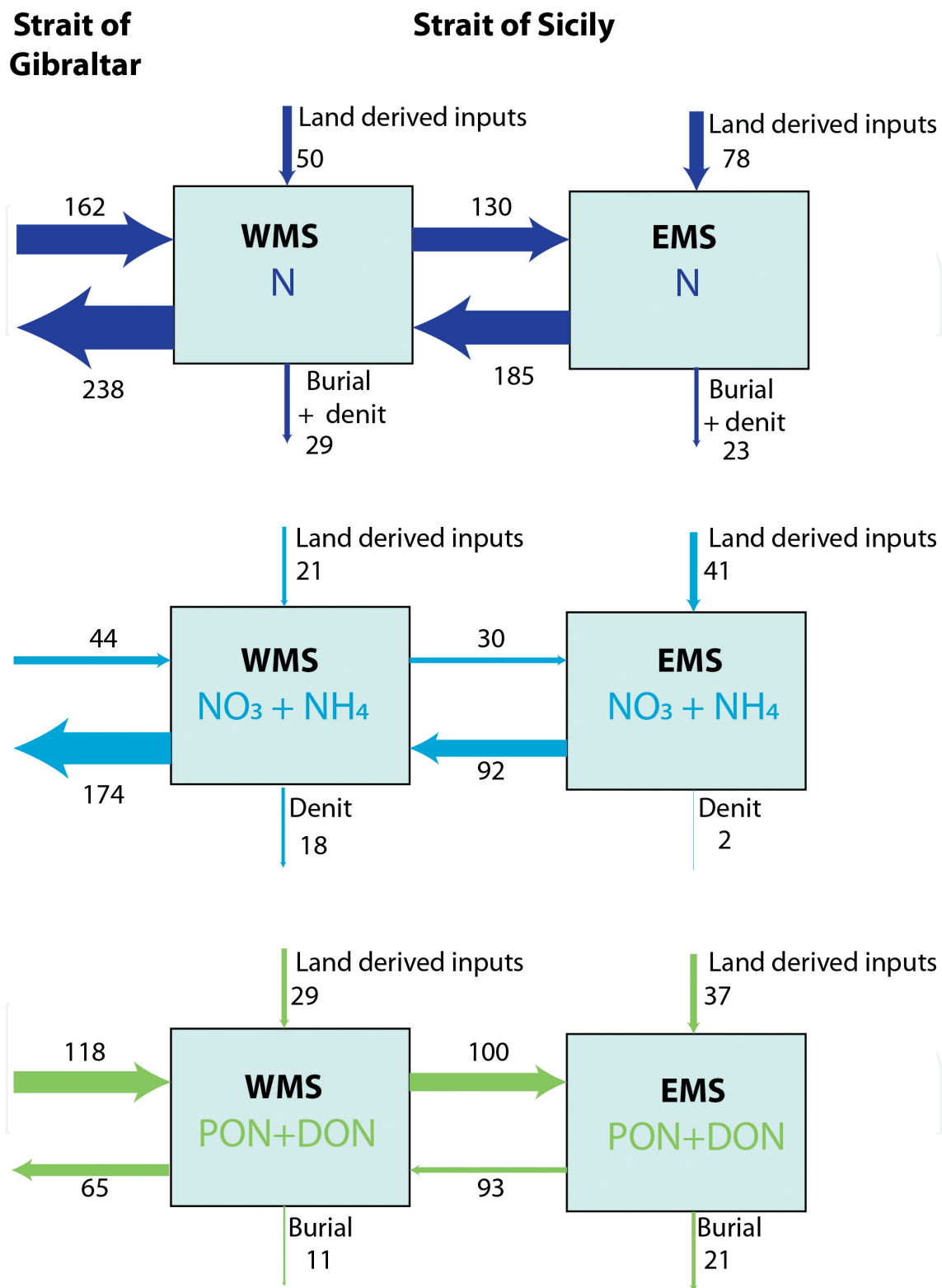


Figure 8. Input and output fluxes of reactive nitrogen (N), dissolved inorganic nitrogen (NO₃ + NH₄) and particulate and dissolved organic nitrogen (PON + DON) to the Western Mediterranean Sea (WMS) and Eastern Mediterranean Sea (EMS). The thicknesses of the arrows scale to the corresponding fluxes. Numerical values are fluxes in units of 10⁹ mol N yr.⁻¹ [17]. Fluxes can be converted to units of mol m⁻² y⁻¹ by dividing them by the surface areas of the WMS and EMS, 815 × 10⁹ m² and 1336 × 10⁹ m², respectively.

whereas more than half of P and N entering the Mediterranean Sea are in their less bioavailable forms, DOP and DON. In total, 88% more dissolved phosphate leaves the Mediterranean Sea through the Strait of Gibraltar than flows in with the Atlantic surface water: the outflow of total P, however, is only 10% greater than the inflow of total P (**Figure 7**). A similar trend is observed for N, with a 47% difference in the total dissolved N flux leaving and entering through the Strait of Gibraltar but four times more dissolved nitrate leaving than entering (**Figure 8**). A similar switch in chemical speciation is also observed at the Strait of Sicily (**Figures 7 and 8**). This emphasizes the need to account for the chemical speciation of nutrient elements, in addition to their total concentrations and fluxes.

2.3. Primary productivity and nutrient cycling: west–east differences

The difference in magnitude of marine-derived sources of P and N to the Western and Eastern Mediterranean Seas is the primary reason behind the west to east gradients in primary productivity and phosphate and nitrate concentrations. Inputs of land-derived sources of P and N are rather similar per unit surface area between the Western and Eastern Mediterranean Seas, yet, per unit surface area, P and N inputs are 3.9 and 3.1 times greater, respectively, for the Western Mediterranean Sea (**Figures 7 and 8**). In the Western Mediterranean Sea, P and N inputs from land are added to a background of P and N that originates from the Atlantic Ocean and the deep layers of the Eastern Mediterranean Sea. In contrast, land-derived inputs into the Eastern Mediterranean Sea are added to a background which is depleted in P and N due to the relatively low concentrations of P and N within the Western Mediterranean surface water entering the Eastern Mediterranean Sea through the Strait of Sicily. Thus, the Western Mediterranean Sea exhibits properties that are intermediate between the ‘normal’ Atlantic waters and the ultra-oligotrophic Eastern Mediterranean Sea waters. In addition to the greater external inputs of P and N to the Western Mediterranean Sea, primary productivity is also supported by upwelling of nutrients from intermediate water into the photic zone, whereas this mechanism is not present in the Eastern Mediterranean Sea. In other words, upwelling provides an additional source of nutrients to the photic zone of the Western Mediterranean Sea compared to the Eastern Mediterranean Sea.

However, higher inputs into the Western Mediterranean Sea do not entirely explain the west to east trends in phosphate and nitrate concentrations observed across the Mediterranean Sea. Despite the much greater dissolved phosphate and nitrate concentrations in the Western Mediterranean Sea, the deep-water DOP and DON concentrations are quite similar in the Western and Eastern Mediterranean Seas. This can be explained by the faster recycling of organic P and organic N back into the dissolved inorganic pools in the Western Mediterranean Sea. Evidence for this faster recycling of organic matter can be seen in the higher population densities of bacteria observed in the Western Mediterranean Sea, which are four to six times greater than in the Eastern Mediterranean Sea, as well as the higher concentrations of alkaline phosphatase, which are about three times greater than in the Eastern Mediterranean Sea [21]. Alkaline phosphatases are a group of enzymes that are designed to break the chemical bonds that hold P locked into organic compounds, thereby releasing dissolved phosphate to seawater. Note that, based on the numbers just provided, there is about twice as much

alkaline phosphatase per bacterial cell in the Eastern Mediterranean Sea. The reason is that the Eastern Mediterranean Sea is more P-starved than the Western Mediterranean. Therefore, the microbial community of the Eastern Mediterranean Sea must work harder to access this extremely limiting nutrient. It does so by producing more alkaline phosphatase per cell: this represents a specific adaptation of the microbial community in the Eastern Mediterranean Sea to the very low availability of P.

2.4. Heterotrophy versus autotrophy

In most areas of the ocean close to land, production of organic matter by phytoplankton exceeds its consumption by respiration, because of the abundant supply of land-derived nutrients. These areas are referred to as *autotrophic*. The excess organic matter is buried in the sediments along the continental margins or exported further offshore into deeper waters. By contrast, many areas of the ocean far from the influence of land are net *heterotrophic*, which means that, integrated over the entire area, more organic matter is respired than produced. Again, the Mediterranean Sea goes against the grain: although it is completely surrounded by land (with the exception of the Strait of Gibraltar), it is heterotrophic. This can be seen for P and N in **Figures 7** and **8**: more DOP and DON enter the Mediterranean Sea from marine and non-marine sources than are removed with the outflow through the Strait of Gibraltar or burial (**Figures 7** and **8**): more DOP and DON is thus mineralized than produced. It was originally suggested by Duarte et al. [22] that the excess dissolved organic matter sustaining heterotrophy in the Mediterranean Sea is supplied by river runoff. Our estimates, however, shows that most of the DOP and DON is delivered by water inflow from the North Atlantic Ocean.

A key factor controlling how much, and how fast, organic compounds are being consumed by bacteria and animals is their so-called lability. It is not just a matter of how much food there is but also what its quality is (i.e. is it prime rib or old shoe leather?). For example, fresh phytoplankton biomass is high-quality food for bacteria and animals. Higher inputs of relatively labile organic matter, both marine and land derived, explain the higher heterotrophy in the Western Mediterranean Sea than the Eastern Mediterranean Sea. More dissolved organic matter enters the Western Mediterranean Sea via the Strait of Gibraltar than enters the Eastern Mediterranean Sea via the Strait of Sicily. In addition, more phytoplankton is produced in the Western Mediterranean Sea, therefore providing a source of fresh organic matter. In comparison to the Eastern Mediterranean Sea, the Western Mediterranean Sea therefore exhibits higher DOP concentrations in its surface waters (more food), but lower DOP in its deep waters, because the higher lability of organic matter in the Western basin leads to its faster consumption (better food).

The net heterotrophy of the Mediterranean Sea is also modulated by the rather unusual timing of the annual phytoplankton bloom, that is, the period during which phytoplankton growth peaks. In many parts of the temperate ocean, the main phytoplankton bloom occurs in spring. Bioavailable nutrients are mixed into surface waters in winter during the cold and often stormy time of the year, but phytoplankton cannot grow rapidly until the depth of mixing decreases and enough sunlight becomes available to carry out photosynthesis. The latter usually happens in spring after the length of day and the angle of the sun have increased sufficiently. By contrast, in the Mediterranean Sea, the phytoplankton bloom occurs in winter

(see **Figure 9**). This is because winter in the Mediterranean Sea is characterized by short periods of cold often windy weather, which causes the surface water to mix and bring up nutrients from below, followed by sunny periods during which mixing temporarily stops and phytoplankton can grow. However, winter is also the time when Mediterranean intermediate and deep waters tend to form. The downwelling surface waters entrain the phytoplankton biomass, hence supplying fresh, and thus labile, organic matter to the bacteria and animals living at greater water depths. Because downwelling occurs when the phytoplankton biomass is at its highest, heterotrophy is relatively more pronounced for the Mediterranean Sea than in areas of the oceans where the phytoplankton bloom takes place in spring.

2.5. Why does the nitrate-to-phosphate ratio of the Mediterranean Sea exceed 16:1?

One of the most remarkable properties of Mediterranean Sea is the significant departure of the deep-water molar nitrate-to-phosphate ratios from the average 16:1 value observed throughout most of the world's ocean ([4, 25]; **Figure 4**). For the Eastern Mediterranean Sea, Krom et al. [26] showed this was due to the combined N/P ratio of the total, non-marine inputs of P and N, which by far exceeds 16:1 (e.g., the ratio of inorganic nutrients supplied through atmospheric deposition is larger than 100:1), and the very limited amount of denitrification. Denitrification is the process in which anaerobic bacteria use nitrate to respire organic matter and produce N_2 gas as a by-product. In the ocean, denitrification is the primary mechanism by which deep-water nitrate-to-phosphate ratios that exceed 16:1 are brought closer to the Redfield ratio [3]. In the Eastern Mediterranean Sea, so little organic matter is produced that there are very few areas where dissolved O_2 is completely consumed. As a result, denitrifying bacteria cannot function, and the excess nitrate-to-phosphate ratio remains. Our mass balance model is able to reproduce the observed ratio of dissolved nitrate to phosphate in the Eastern Mediterranean deep water by accounting for the external supply and the transformations and transport of the two nutrient elements [17]. The results invalidate the previous explanation attributing the high nitrate-to-phosphate ratio to high rates of nitrogen fixation in the Eastern Mediterranean Sea. This is consistent with measured rates of nitrogen fixation that are amongst the lowest observed anywhere in the global ocean [27, 28].

The model calculations further demonstrate for the first time that the higher than Redfield nitrate-to-phosphate ratio of the Western Mediterranean Sea deep water is similarly caused by the high N/P ratio of the external nutrient supply combined with low levels of denitrification [17]. Although in our model some nitrogen fixation does occur in the Western Mediterranean Sea, compared to none in the Eastern Mediterranean Sea, it is more than offset by a 12 times greater rate of denitrification per m^2 sea surface area. The dissolved nitrate-to-phosphate ratio of Western Mediterranean deep water is nonetheless lower than that of Eastern Mediterranean deep water largely because of a lower total N/P ratio of the external nutrient inputs, in particular due to the inflow of low N/P North Atlantic surface water.

2.6. Mediterranean nutrient cycling: unravelling the importance of different processes

A useful *in silico* exercise that can be performed with the biogeochemical mass balance model is to remove one process at the time and observe the resulting effect on the cycling of

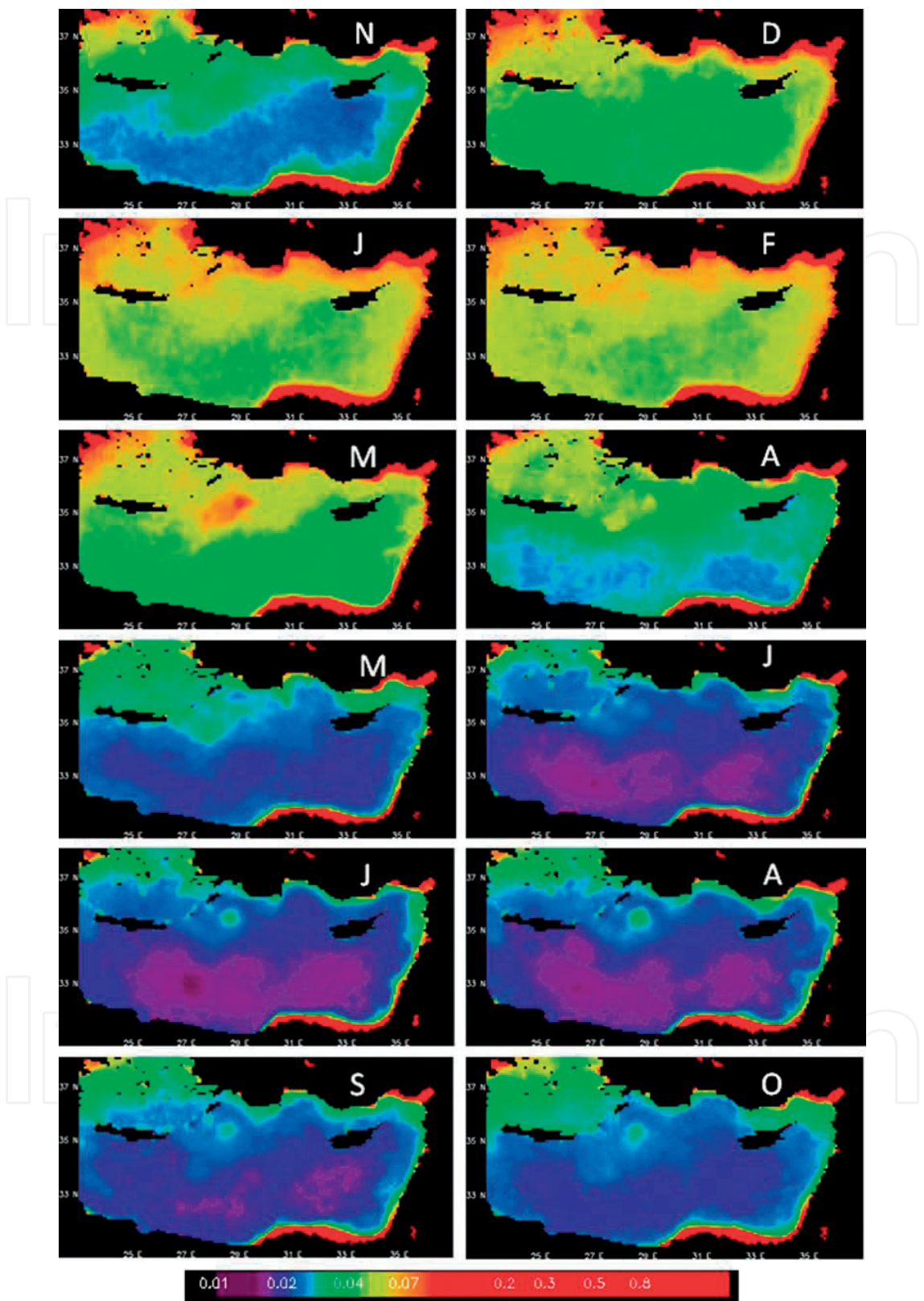


Figure 9. Monthly SeaWiFS ‘climatological’ images of chlorophyll from November to October. The images are based on input data from September 1997 to August 2004. Concentrations of chlorophyll-a were computed using the Bricaud et al. [23] algorithm for the Mediterranean Sea [24]. The images were provided by Steve Groom (NERC Earth Observation Data Acquisition and Analysis Service, Plymouth). This figure is available in colour in the online version of this chapter.

P and N [17]. For instance, we found that if the atmospheric input of bioavailable P and N is removed, the model yields deep water-dissolved nitrate-to-phosphate ratios of 15–16 for both the Western and Eastern Mediterranean Seas, despite the large differences in the starting ratios (21:1 and 28:1). By contrast the removal of P and N inputs associated with submarine ground water discharge, rivers or direct wastewater inputs has no significant effects on the deep-water nitrate-to-phosphate ratios. However, when the P and N inputs via the Strait of Gibraltar are removed, then the deep-water ratios increase to 53:1 (Western Mediterranean Sea) and 69:1 (Eastern Mediterranean Sea). This suggests that the higher than Redfield nitrate-to-phosphate ratios observed in the Mediterranean Sea are ultimately driven by the high N/P ratio of the external nutrient input via atmospheric deposition but also that without dilution by the low N/P nutrient supply from the North Atlantic Ocean, Mediterranean-dissolved nitrate-to-phosphate ratios could be even larger than actually observed.

Another model application consists in calculating by how much the denitrification rate would have to increase to bring the deep-water nitrate-to-phosphate ratios of the Mediterranean Sea down to the Redfield value (16:1). The results indicate that the denitrification rate in the Western Mediterranean Sea would have to be 2.2 times higher than in 1950 (increasing to $0.05 \text{ mol N m}^{-2} \text{ y}^{-1}$), while in the Eastern Mediterranean Sea, it would have to be 7 times higher than in 1950 (increasing to $0.01 \text{ mol N m}^{-2} \text{ y}^{-1}$). In the global ocean, denitrification rates mostly fall in the range of $0.04\text{--}0.10 \text{ mol N m}^{-2} \text{ y}^{-1}$ [29, 30]. This means that if the Mediterranean Sea supported rates of denitrification of the same order of magnitude as the rest of the oceans, then its deep waters would approach ‘normal’ Redfield ratios around 16:1. An important conclusion is that the unique nutrient distributions in the Mediterranean Sea are not due to some unknown process not encountered elsewhere in the oceans, but rather to ‘normal’ ocean processes—but then in an unusual combination.

3. Environmental implications

3.1. Anthropogenic nutrient enrichment

During the second half of the twentieth century, land-derived emissions of P and N to the Mediterranean Sea reached levels 2.6 and 2.3 times higher than in 1950, respectively ([19, 31]; **Figure 10**), as a result of the rapid growth of coastal populations and intensifying economic activities. The huge increases in nutrient supply by rivers and via atmospheric deposition, however, have had relatively little impact on the open waters of the Mediterranean Sea, with only a 10–20% increase in primary productivity (**Figure 10**). The reason is that the Mediterranean Sea has a very efficient natural buffer to counter increases in the supply of nutrients, especially in the Eastern Mediterranean Sea. Newly added nutrients to the surface water are rapidly transferred to the deeper-water layers, either by downwelling of surface water or settling of biological debris. Because of the anti-estuarine circulation, much of the additional dissolved P and N in the intermediate water of the Eastern Mediterranean Sea is removed by outflow through the Strait of Sicily, while most of the rest accumulates in the deep-water layer. A similar scenario plays out in the Western Mediterranean Sea with most

of the additional P and N either exported to the North Atlantic Ocean or stored in the deep water, rather than contributing to primary production [19].

An additional result of the very low productivity is that the O_2 contents of the waters of the Mediterranean Sea remain elevated: no permanent or seasonal areas of hypoxia are observed in the open Mediterranean Sea. This contrasts with the Baltic Sea, which receives comparable influxes of external pollutant nutrients per unit area but with very different consequences. There are major eutrophication problems in the Baltic Sea including areas of hypoxia and toxic algal blooms. This does not mean there are no problems of excess nutrients in the Mediterranean Sea. There are, but they tend to be local and restricted to nearshore areas, such as the salt water lagoons of the Nile delta and Venice lagoon. In the past, coastal areas of the North Adriatic Sea were plagued by eutrophication problems, which have now been much reduced. However, offshore basin-wide, nutrient enrichment is not a problem, because the system is efficiently buffered. Model projections into the future show that this result is robust. Even taking into account the various possible changes in physical circulation and P and N emissions during the remainder of the twenty-first century, model simulations predict that the Mediterranean Sea will remain oligotrophic [19].

Similar considerations apply to the environmental impacts of mariculture, which is on the rise in the Mediterranean region as wild fish populations decrease. In most cases, concerns about excess nutrients being released by mariculture are likely unfounded given the very low natural productivity of the surrounding waters and the rapid assimilation of added nutrients into the regional food web. While other issues may arise, such as those related to the dispersion

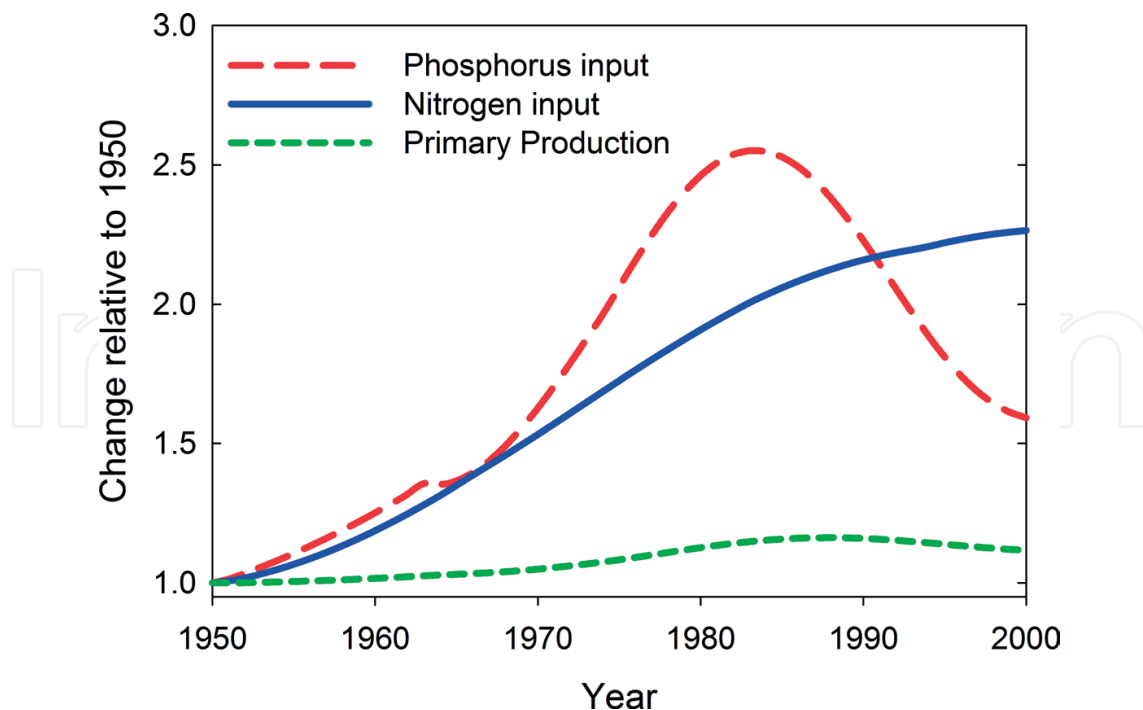


Figure 10. Reconstructed relative changes of land-derived reactive phosphorus and nitrogen inputs to the Mediterranean Sea and corresponding changes in primary productivity, from the year 1950 to 2000. Data from Powley [19].

of pharmaceuticals or the possible introduction of invasive species, it seems clear that for any reasonable fish loading, mariculture will not lead to significant regional increases in nutrients and eutrophication [32].

3.2. Will ongoing global climate warming cause hypoxia in the Mediterranean Sea?

Changes in the *thermohaline circulation* can profoundly affect the biogeochemistry of the Mediterranean Sea. A good example from the past is sapropels, that is, organic-rich sediments that were deposited periodically between 6000 years and 13.5 million years ago, mostly in the Eastern Mediterranean Sea [33]. In deep sediment cores, sapropels occur as distinct dark layers separated from one another by intervals of lighter coloured, organic-poor sediments similar to those accumulating in the deep basins of the Mediterranean Sea at the present time. The sapropels are typically laminated and lack evidence of bottom dwelling animal life, implying they were deposited at times of *anoxia* when no (or very little) dissolved O_2 was present in the deep waters. The lack of O_2 in turn limits the degradation of organic matter at the seafloor, thereby leading to the accumulation of organic-rich sapropel. In contrast, today the deep waters of the Mediterranean Sea are well oxygenated (i.e. they are *oxic*), and O_2 -respiring bacteria decompose most of the organic matter that sinks to the bottom.

Extensive studies of sapropels, in particular those carried out on the most recently deposited sapropel (Sapropel S-1), conclude that the transitions in the deep-water *redox* chemistry of the Eastern Mediterranean Sea that accompanied the initiation and cessation of sapropel formation (i.e. the alternations between oxic and anoxic deep waters) were linked to changes in thermohaline circulation, which, in turn, were caused by natural climate fluctuations [34]. This raises concerns about the ongoing warming trend in the Mediterranean region, which could potentially trigger a reappearance of hypoxic or anoxic bottom waters in the Mediterranean Sea. Dwindling O_2 levels could have devastating consequences for marine life at the seafloor, as well as for water quality throughout the water column (under O_2 -depleted conditions, microorganisms generate toxic by-products, such as *hydrogen sulphide*).

Predicting the effects of anthropogenic climate change on the thermohaline circulation of the Mediterranean Sea, however, is far from straightforward. The difficulty resides in predicting how climate change will affect the *density* of Mediterranean surface waters. The rate at which deep water forms is directly related to the density contrast between the surface and deeper-water layers: the denser the surface water, the faster it sinks. Climate projections tend to agree with relatively high confidence that the Mediterranean region will experience higher temperatures and reduced rainfall in the coming decades [35]. The problem is that these changes have opposite effects on the density of seawater: higher temperatures decrease the density, while less rain and higher evaporation rates increase the density. Thus, depending on which effect wins out, thermohaline circulation under a warmer and drier climate could either accelerate or slow down. So far, there is no consensus in which direction the circulation of the Mediterranean Sea may be heading.

In order to explore the potential impacts of climate change on the oxygenation of the deeper waters of the Mediterranean Sea, we created a model of dissolved O_2 cycling similar to the nutrient model presented earlier in this chapter [18]. The model accounts for the consumption

of O_2 by respiration in each water layer of the Western and Eastern Mediterranean Seas. The model-calculated O_2 concentration within each of the intermediate and deep-water layers then reflects the balance between the supply of O_2 by sinking (O_2 -rich) surface water and consumption of O_2 by respiration. The dissolved O_2 concentration in the surface waters remains close to equilibrium with the O_2 concentration in the atmosphere, which in the model calculations is held constant.

The scenarios tested with the O_2 model correspond to the extreme effects of anthropogenic climate change on the physical circulation of the Mediterranean Sea, based on the work of Somot et al. [36] and Adloff et al. [37]. The extremes range from a slowing down to a speeding up of the Mediterranean thermohaline circulation, that is, from a weakening to a strengthening of the deep-water formation processes. The model calculations further account for the effects of increasing temperatures and salinity on the solubility of O_2 and respiration. Increasing temperatures reduce the amount of O_2 that dissolves in surface waters and thus reduce the O_2 supply to the interior of the Mediterranean Sea by deep-water formation. At the same time, higher temperatures stimulate microbial activity and thus increase respiratory O_2 consumption rate. The model scenarios were run until new steady states were reached. The new steady-state O_2 levels in the deep-water layer are shown in **Figure 11**, together with those obtained 100 years after the deep-water formation rates are switched to their new values.

Figure 11 also displays results obtained with two alternative representations of the O_2 respiration rate. The first formulation ('no feedback') assumes that the rate of O_2 consumption only depends on the availability of O_2 to the microorganisms. The chosen mathematical expression ensures that O_2 respiration slows down and ultimately stops when the dissolved O_2 concentration approaches zero. In the second formulation ('feedback'), the rate of O_2 respiration also depends on the availability of *energy substrates* that can be used during respiration. In deep ocean waters, the primary energy substrates accessible to microorganisms are dissolved organic carbon compounds (also referred to as DOC). The 'feedback' representation thus provides a more complete representation of O_2 respiration than the 'no-feedback' representation. As discussed below, comparison of results obtained with the two formulations illustrates the importance of *negative feedbacks* in marine environments.

The O_2 concentrations in the intermediate water layers exhibit little change (<10%) in response to the imposed changes in circulation. The largest changes in O_2 concentrations are observed for the deep-water layers in the scenario where climate warming causes a significant slowing down of the thermohaline circulation, as shown in **Figure 11**. Furthermore, the effect is most pronounced in the Eastern Mediterranean Sea where the deep-water O_2 concentration is predicted to drop below 50 μM (compared to present-day values around 200 μM). However, it takes at least 600 years after the change in circulation for hypoxic conditions to develop, that is, for the O_2 concentration to cross the threshold value of 2 mg/l (62 μM) below which the lack of O_2 may severely harm marine life. Interestingly, even when the deep waters of the Eastern Mediterranean Sea become hypoxic, those of the Western Mediterranean Sea remain oxic. Such a contrast in deep-water oxygenation between the two basins also characterized most periods of sapropel formation during which oxic conditions persisted in the deeper parts of the Western Mediterranean Sea. Furthermore, a slowing down of the thermohaline circulation

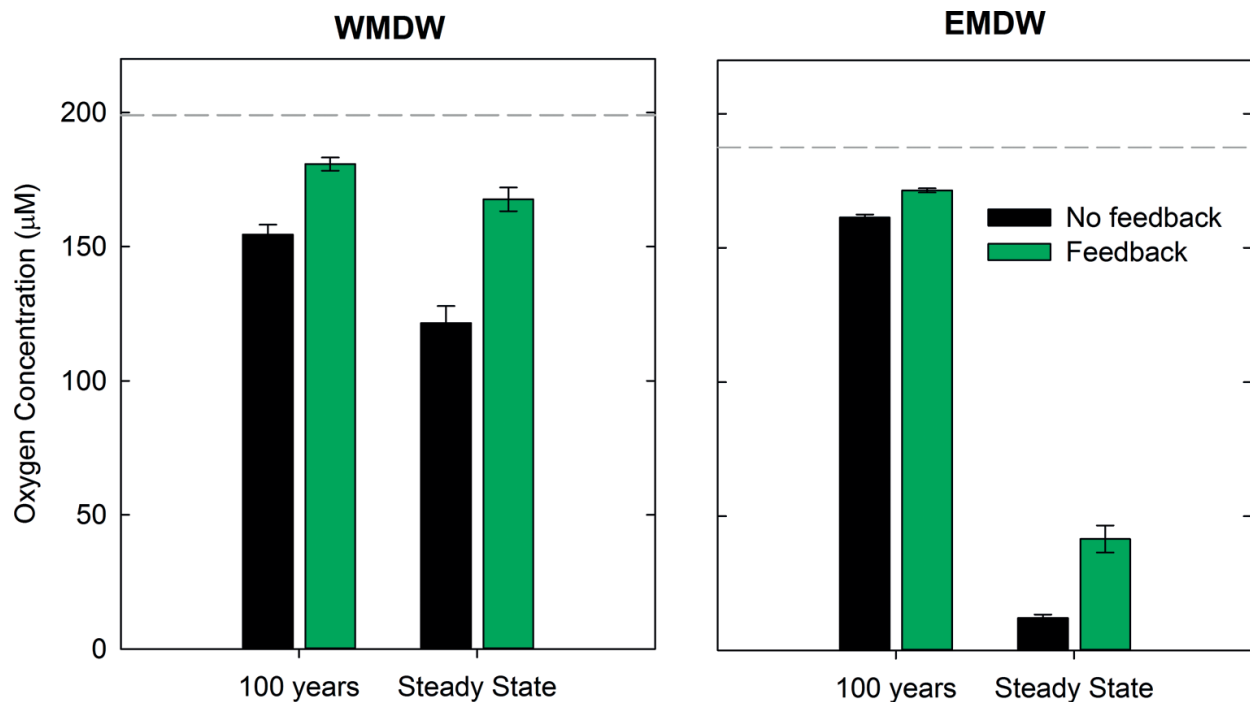


Figure 11. Model-predicted dissolved oxygen (O_2) concentrations in the Western Mediterranean deep water (WMDW) and Eastern Mediterranean deep water (EMDW), for the decreased thermohaline circulation climate change scenario. The dashed horizontal line represents the O_2 concentrations under the current thermohaline circulation regime. The two sets of bars in both panels are results obtained either 100 years after switching to the slower circulation regime or after the O_2 concentrations reach their new steady-state values. 'No feedback' corresponds to the model calculations ignoring the dissolved organic carbon (DOC) feedback on deep-water respiration, while 'feedback' corresponds to the results when the feedback is included. See text and **Figure 12** for more details. Error bars reflect uncertainty of temperatures and salinity in climate change projections and thus O_2 solubility and microbial rate kinetics. Data from Powley et al. [18].

similar to that simulated here has been proposed to have been a driver for sapropel formation [34, 38]. The analogy with the current warming trend, however, is only partially valid: all the evidence strongly suggests that the more recent sapropels (including S-1) were deposited under a wetter and colder climate during a period of sea level rise following the last ice age.

The model calculations also highlight a possible self-regulating negative feedback that minimizes the impacts of changes in the thermohaline circulation on the oxygenation of the deeper waters of the Mediterranean Sea. How the feedback works is illustrated in **Figure 12**. It results from the fact that deep-water formation not only supplies surface water enriched in dissolved O_2 but also in bioavailable DOC, that is, the two ingredients that sustain microbial respiration. This is not unlike the bloodstream in the human body, which supplies both O_2 and DOC in the form of glucose to our cells. If the thermohaline circulation weakens, and hence deep-water formation decreases, less O_2 is transferred to the deeper layers of the Mediterranean Sea but also less DOC. The outcome is less biological O_2 consumption in the model runs where the rate of respiration depends on both the availability of O_2 and DOC (i.e. the 'feedback' results in **Figure 11**). In other words, the decreased supply of O_2 by slower deep-water formation is in part compensated by the reduced supply of DOC and, hence, the reduced consumption of O_2 . Similarly, a more vigorous thermohaline circulation supplies higher amounts of both O_2 and DOC to the deeper layers

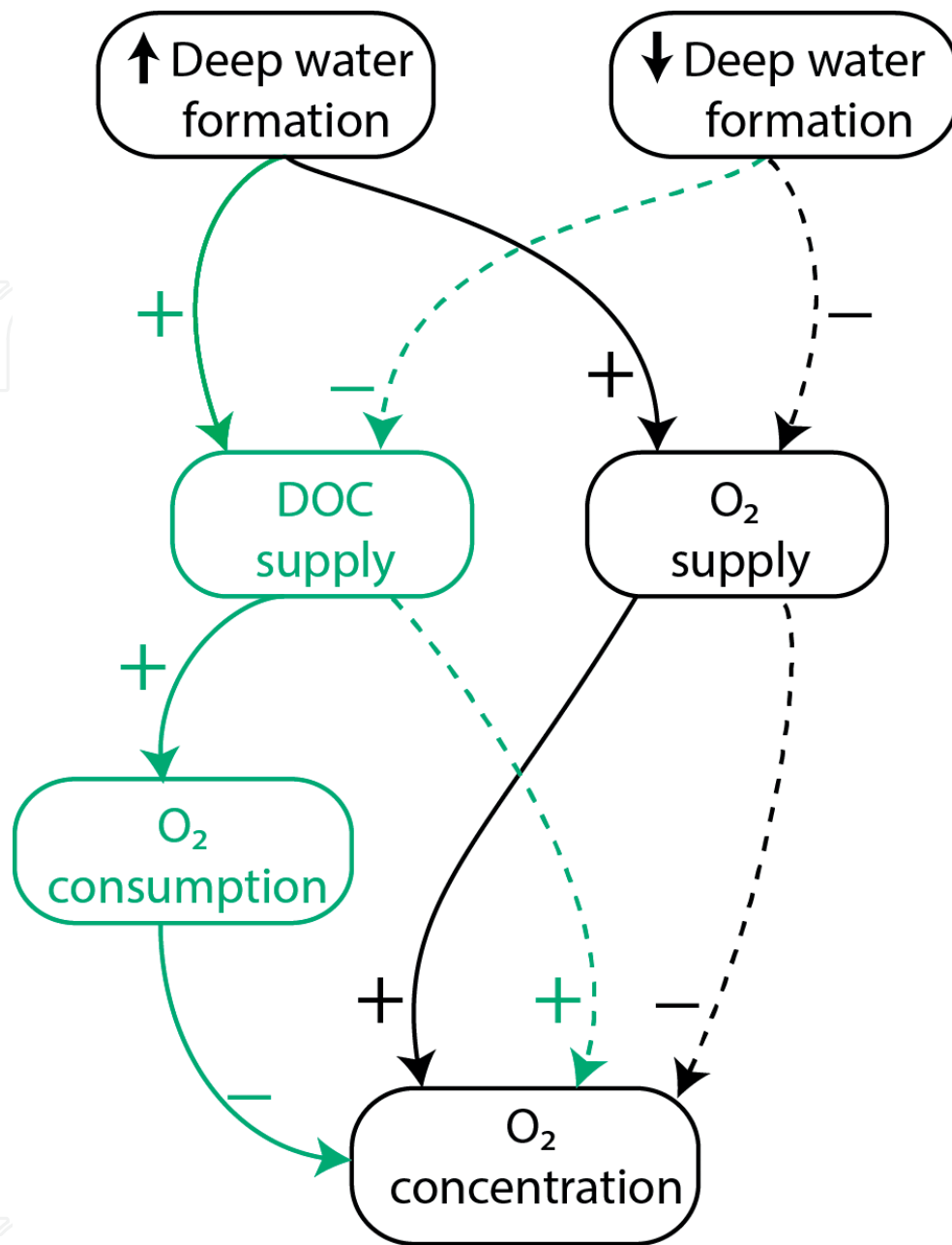


Figure 12. Schematic illustration of the effects of deep-water formation rates on deep-water oxygen (O₂) concentrations. Solid arrows show the effects of increased deep-water formation (stronger thermohaline circulation), and dashed arrows show the effects of decreased deep-water formation (weakened thermohaline circulation). Black arrows and boxes identify the effects of changes in the thermohaline circulation without the DOC feedback, while green (grey in print version) arrows and boxes show the additional effects of including the dissolved organic carbon feedback on O₂ consumption. This figure is available in colour in the online version of this chapter.

of the Mediterranean Sea. The higher deep-water O₂ concentration that may be expected from the enhanced supply of O₂, however, is offset by the increased supply of DOC, which increases the rate of O₂ consumption. Negative feedbacks such as the one illustrated here are commonly observed in biogeochemical systems. Nonetheless, the O₂-DOC feedback for deep-water oxygenation of the Mediterranean Sea remains, at present, speculative and requires further investigation.

Biogeochemical mass balance (box) models.

Box models represent a given system as a series of interconnected reservoirs or boxes. The state variables of the model are the masses, M_i , in the reservoirs. For example, one of the state variables in the nutrient model is the mass of dissolved organic P (DOP) in the intermediate water layer of the Eastern Mediterranean Sea. Ordinary differential equations (ODEs) describe the fluxes of matter in and out of the reservoirs as a function of time, t . Thus, in **Figure B.1**, there is an input flux, F_{in} , into the box and output flux, F_{out} , away from the box.

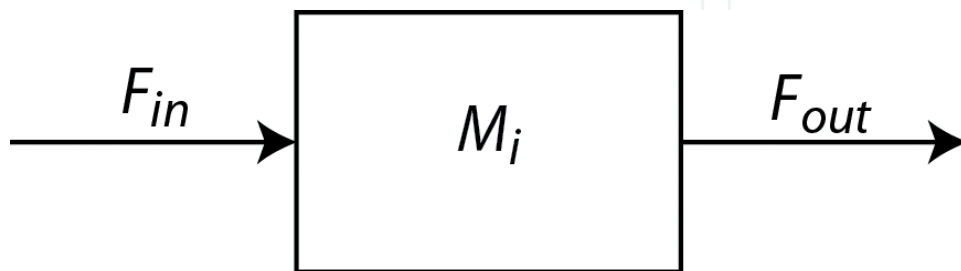


Figure B.1 Box model: the box or reservoir represents the mass of the variable of interest (M_i) and fluxes in (F_{in}) and out (F_{out}) of the reservoir.

Note that the fluxes may correspond to the physical transport of the state variable (e.g. DOP in Eastern Mediterranean intermediate water) from or to another physical location (e.g. DOP moving from the Eastern Mediterranean intermediate water layer into the Western Mediterranean Sea via the Strait of Sicily) or the transformation of the state variable at a given physical location (e.g. the mineralization within the Eastern Mediterranean intermediate water layer of DOP into dissolved inorganic phosphate).

The mass conservation equation describing the time evolution of the state variable, M_i , in **Figure B.1** is then given by

$$\frac{dM_i}{dt} = F_{in} - F_{out} \quad (1)$$

where the fluxes are given in units of mass per unit time. For each reservoir in the model, an ODE of the form of Eq. (1) is derived. For example, **Figure B.2** presents the dissolved phosphate reservoir in the deep-water layer of the Eastern Mediterranean Sea.

The corresponding ODE is

$$\frac{dPO_4^{EMDW}}{dt} = min+dwf-up \quad (2)$$

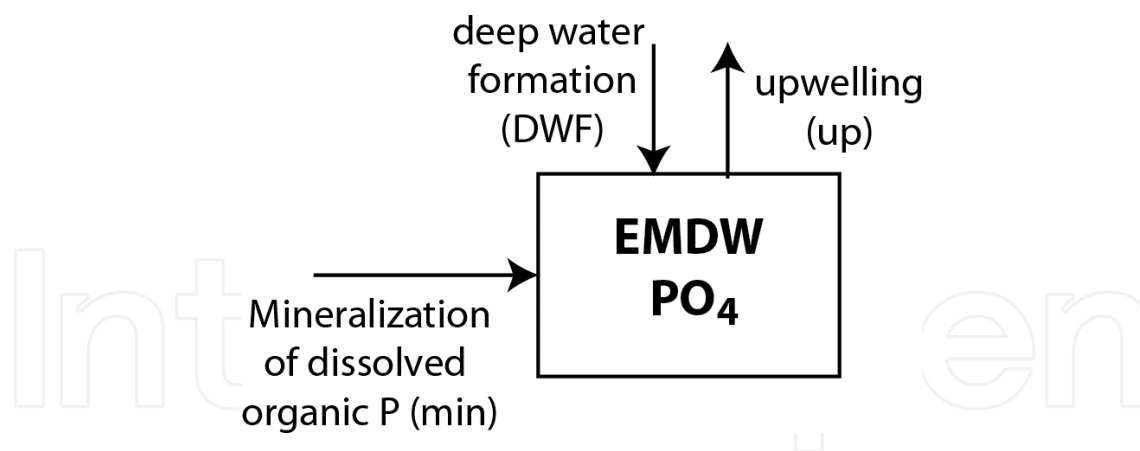


Figure B.2 Input and output fluxes to the Eastern Mediterranean Sea deep water (EMDW) dissolved phosphate (PO_4) reservoir in the nutrient model.

For each term on the right-hand side of Eq. (2), a mathematical expression must be assigned. When all the mass conservation equations are specified, one for each reservoir, the system of ODEs is solved as a function of time, t , using a numerical method. Mathematically, a system of ODEs can only be solved if initial conditions are specified, that is, the values of the state variables, M_i , must be known at some given initial time (i.e. at $t = 0$). In our mass balance calculations, we impose the estimated masses in the P and N reservoirs in 1950 as the initial conditions.

A special condition for any dynamic model (i.e. a model with time as an independent variable) is that of the steady state. For a box model, this means that, for each reservoir, the input fluxes exactly balance the output fluxes or

$$\frac{dM_i}{dt} = 0 \quad (3)$$

which is equivalent to stating that all state variables remain constant. This is the condition we assign to the 1950 P and N cycles in the Mediterranean Sea.

While the mass balance equations are written in terms of the chemical masses in the different reservoirs (M_i), the results of the calculations are compared to measured concentrations (C_i) in the different water layers of the Mediterranean. The factor that allows us to convert between M_i and C_i is the volume of the corresponding water layer.

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corrections to an earlier draft of this text. The senior author (MDK) was inspired while writing this text by some of the tunes in the Pirates of Penzance.

Glossary of terms

Anti-estuarine circulation This unusual form of circulation is typified by what happens in the Mediterranean Sea. Anti-estuarine circulation is where surface water flows into a basin and deeper-water flows out of the basin: estuarine circulation is the opposite.

Anoxia Occurs when there is no dissolved oxygen (O_2) left in a given water body.

Autotrophic When, in a given environment, more organic matter is produced as a result of photosynthesis than is consumed through respiration.

Denitrification A microbial process in which bacteria use nitrate (rather than oxygen) to respire organic matter to generate energy for their life processes. It only takes place in locations with very low (zero) oxygen and a supply of nitrate. The waste product of this reaction is dinitrogen gas.

Density Refers to how much mass is in a given volume (mathematically defined as mass/volume). In the oceans, temperature and salinity are the two main properties that influence the density of water. The higher the temperature, the lower the density of water as the water molecules have higher energy and are more spread out. Likewise the higher the salinity of water, the denser the water because more salt is present per unit volume of water.

Downwelling The deep water of the ocean is formed in specific locations almost always in the polar regions. These locations are where surface water becomes so cold and dense that it 'downwells' and fills the deep basins of the global ocean. The most important of these downwelling regions are in the North Atlantic Ocean between Greenland and Norway and in the waters around Antarctica.

Energy substrates Chemical substances that can be broken down during respiration to provide the energy required by organisms. The most common energy substrates are organic compounds containing carbon, hydrogen and oxygen and frequently phosphorus and nitrogen. Some major groups of organic compounds include carbohydrates, fats, proteins and amino acids.

Eutrophication A form of water pollution. Cultural or anthropogenic eutrophication occurs when excessive phosphorus and nitrogen from sources such as fertilizers and wastewater discharges run into a body of water. This encourages the growth of algae and other aquatic plants. As the plants die, bacterial degradation occurs (the plants decay) which consumes dissolved oxygen within the water. In extreme situations this can result in all the dissolved oxygen being consumed, leading to mass mortalities of fish and other marine organisms.

Heterotrophic When, in a given environment, more organic carbon is consumed by respiration than is produced by photosynthesis.

Hydrogen sulphide (H_2S) A colourless volatile compound that has a rotten egg smell and produces black-coloured sediments. It is produced from sulphate (SO_4) as a result of respiration under anoxic conditions when other higher energy-producing electron acceptors such as oxygen and nitrate have been entirely consumed. It is a toxic substance.

Hypoxic When the dissolved oxygen (O_2) content in a body of water is so low ($<62 \mu M$ or 2 mg/l) that it is detrimental to the animals that live there.

Marine snow Is formed by aggregates of plankton and debris of other organic matter particles together with dust and other inorganic particles held together in a matrix of gel-like material. Together the aggregates are heavy enough to settle into deeper water rather like 'snow'.

Mineralization The transformation of dissolved organic phosphorus (DOP) and dissolved organic nitrogen (DON) back into dissolved inorganic P (phosphate) and N (nitrate). This process is primarily the result of enzymatic hydrolysis.

Negative feedback When the response of a system to a given perturbation (change) acts to counteract the initial perturbation and thus reduce its effect.

New production The primary production supported by nutrients added externally to the photic zone of the ocean, rather than by nutrients that are recycled by mineralization of organic matter produced within the photic zone.

Nitrogen fixation A bacterial process, which converts dinitrogen gas to organic nitrogen. It is a very ancient process having evolved in the early Precambrian and is the dominant natural source of fixed nitrogen for life processes.

Ocean gyres There are very large slowly spinning bodies of water in the major basins of the world's oceans. There are two major gyres in the Northern Hemisphere and three in the Southern Hemisphere. In the North Atlantic Ocean, the current that defines the western boundary of the gyre is called the Gulf Stream. In general, downwelling occurs in the centre of the ocean gyres, and these are the least productive parts of the global ocean.

Oligotrophic Refers to water bodies that have very low primary production, typically because they are severely limited by a lack of dissolved inorganic nutrients. Oligotrophic water bodies are defined as having chlorophyll concentrations less than 0.1 mg m^{-3} .

Oxic Bodies of water with plentiful dissolved oxygen (O_2): typically more than $62 \mu M$ or $2 \text{ mg } O_2$ per litre water.

Photic zone The area at the top of the ocean that receives sunlight and so is the area where phytoplankton grow.

Phytoplankton Microscopic marine plants which grow in the surface layers of the ocean. They are the main plant life in the ocean and form the base of the marine food chain.

Primary production Phytoplankton growth is called primary productivity. Phytoplankton carry out photosynthesis: sunlight is used to convert carbon dioxide and water plus other nutrient elements into organic matter. This forms the base of the food chain in the ocean. Organisms that photosynthesize are called autotrophs. Phytoplankton are autotrophs.

Redox This term is shorthand for reduction–oxidation reaction, that is, a chemical reaction in which the oxidation states of atoms are changed. Any such reaction involves both a reduction process and a complementary oxidation process. Photosynthesis and respiration are redox processes.

Respiration The chemical reactions by which cells produce energy. It involves the breakdown of energy substrates: often organic compounds: with the use of an oxidant. When molecular oxygen (O₂) is present, it is the preferred oxidant for respiration; when it is absent, microorganisms can use other oxidants, including nitrate.

Solubilization The transformation of particulate organic phosphorus (POP) and particulate organic nitrogen (PON) to dissolved organic phosphorus (DOP) and dissolved organic nitrogen (DON), respectively. A variety of processes are lumped together in this pathway including hydrolysis, passive diffusion or active exudation from phytoplankton, viral- and bacterial-induced cell lysis, sloppy feeding by zooplankton and bacteriavory.

Thermohaline circulation The large-scale circulation that is caused by density differences of oceanic water. The density is controlled by changes in water temperature (thermo) and salinity (haline). Thermohaline circulation of the global ocean is also called the global conveyor belt. The thermohaline circulation is driven by the downwelling of dense water, while water is returned to the surface by upwelling.

Upwelling The opposite of downwelling. There are regions of the ocean where deep and intermediate waters are 'upwelled' to the surface of the ocean. Since they carry with them high concentrations of dissolved macronutrients, these are areas of high primary productivity. Two important upwelling regions are off the coast of Peru and off the coast of Namibia.

Author details

Helen R. Powley¹, Philippe Van Cappellen¹ and Michael D. Krom^{2,3*}

*Address all correspondence to: M.D.Krom@Leeds.ac.uk

1 Ecohydrology Research Group, Water Institute and Department of Earth and Environmental Sciences, University of Waterloo, Waterloo, Ontario, Canada

2 Department of Marine Biology, Charney School of Marine Sciences, University of Haifa, Mt Carmel, Haifa, Israel

3 School of Earth and Environment, University of Leeds, Leeds, United Kingdom

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