



The Mediterranean pelagic ecosystem response to physical forcing

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Abstract

The effects of physical forcing on pelagic ecosystem are studied using numerical models, in which ecological and physical processes are coupled. The implications of the mathematical formulation of coupling are discussed, outlining the different parameterisation in combining spatial and temporal scales. Existing 3D and 1D numerical models of the Mediterranean Sea are presented. The results are used to assess the respective roles of light and nutrients in limiting phytoplankton growth and to suggest that the East–West trophic gradient in Mediterranean is the result of the superposition of biological pump and estuarine inverse circulation. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The primary energy source for the ecosystem comes from external physical forcing. Solar radiation is the negentropy input (editor note: i.e. it creates order) that supports organized forms of life in the different levels of the food chain. Even though the incoming solar radiation at the atmospheric boundary is remarkably deterministic, the instabilities of the atmospheric dynamics generate a large number of expressions of climatic conditions (Pedlosky, 1987). This variability induces direct momentum and vorticity inputs into the ocean, and the effects of radiative and mass fluxes greatly influence the thermodynamic properties of the ocean. Variations in the turbulent regime, mixed layer depth, temperature and salinity all affect biological processes locally, but they can also be transferred remotely by mean flow and eddy fluxes. The influence of physical forcing on the ecosystem dynamics is related to the typical scales of the interacting processes (Mann & Lazier, 1991). Numerical models now seem to be mature enough to address the ambitious task of reproducing, explaining, and possibly predicting, the evolution of marine ecosystems and their response to the variability of physical forcing. A number of numerical coupled models have been developed for the World Ocean in order to establish which are the critical climatological, seasonal and interannual variabilities of the ecosystem at both a global and a regional scale (for an overview see Hofmann & Lascara, 1998). These exploit the more detailed knowledge of the ocean and atmosphere circulation that is now available, in terms of both large multidisciplinary data sets (Conright, Levitus & Boyer, 1994; Karl & Michaels, 1996) and so produce more realistic predictive models.

Surprisingly the Mediterranean, in spite of its favourable position, has received less attention and only recently have numerical studies of the Mediterranean ecosystem been carried out. The relative novelty of pelagic eco-hydrodynamic models dedicated to the Mediterranean is reflected in recent review papers. In a survey of ecological models (Totterdell, 1993) only one paper out of more than a hundred explicitly addressed the Mediterranean. Olson and Hood (1994), when reviewing various combinations of physical and biological models used to determine the distributions of organisms in the oceans, did not quote any papers related to the Mediterranean Sea. In an overview of interdisciplinary models for marine ecosystem studies, Hofmann and Lascara (1998) mentioned only two works pertaining to the Mediterranean. In recent years, multidisciplinary projects have been specifically targeted at Mediter-

anean Sea and are now providing the necessary conceptual background and data to help fill this gap.

The aim of this study is to put forward the theoretical background to the coupling and to exploit this tool to relate oligotrophy and seasonal cycles to the dynamics of the physical forcing.

First, the ecosystem dynamics specific to the Mediterranean Sea will be introduced in terms of its physiography and physical forcing. We assume that numerical simulations are an effective tool when used in this multidisciplinary context. A formal derivation of coupling of models will be presented in order to elucidate the major assumptions made, often implicitly, in the design of coupled ecohydrodynamic models, with particular emphasis on ongoing modelling efforts in the Mediterranean Sea. In light of the general conclusions, the explanatory capability of one- and three-dimensional coupled models is then applied to explain the spatial and temporal distribution of nutrients and phytoplankton on climatological and seasonal scales in the Mediterranean basin. In the conclusion, a brief summary of the achievements and of the gaps in our understanding of the Mediterranean is given, along with some guidelines for future model improvements.

2. Characterization of the Mediterranean Basin

The Mediterranean is an elongated semi-enclosed basin with significant exchanges only at the Gibraltar Strait. As first recognised by Thomsen (1931), it is known to be the largest oligotrophic area in the world. Its inverse estuarine circulation contributes to the maintenance of this trophic regime. At Gibraltar the bottom layer is exporting more nutrients than are received from the Atlantic via the surface layer; the net loss of nitrate has been estimated to be from 1.25 Mtons/year (Sarmiento, Herbert & Toggweiler, 1988) to 3.11 Mtons/year (Béthoux, 1979).

The thermohaline cell that controls the upper circulation of the Mediterranean is driven by the slight deficiency of water and the heat budgets, which are compensated by the exchanges through the Gibraltar Strait (Garrett, 1996; Gilman & Garrett, 1994; Bryden & Kinder, 1991). The basin is virtually landlocked, and contains relatively small areas of coastal shelves; notable exceptions are the Catalan and Tunisian shelves, so interactions between the deep water and the coastal areas are unusually direct. The trophic conditions are different in the regional seas (Adriatic and Aegean) where the shelves are well developed and where external sources (the Po and other Italian and Albanian rivers in the North Adriatic, the Black Sea inflow in the North Aegean) act to mitigate the oligotrophy. However, these riverine inflows into regional seas do not significantly affect the pelagic ecosystem on a basin scale, and there are few direct riverine inputs (Rhone, Ebro and Nile) which discharge directly into the main basin.

The Mediterranean is divided in two sub-basins, linked via the Sicily Strait, which has a shallow sill that helps to decouple the hydrodynamic and ecological conditions in the two subbasins. The external exchanges of the sub-basins are (besides between each other) with the Atlantic Ocean via the Gibraltar Strait in the Western Mediter-

ranean and with the Black Sea via the Dardanelles and Bosphorus Straits in the Eastern Mediterranean. All the regional seas communicate directly with the Eastern Mediterranean, there are no counterparts linking with the Western Mediterranean. The two sub-basins are offset latitudinally, the Western Mediterranean is encompassed by 35°N and 44.5°N and the Eastern Mediterranean by roughly 30°N and 40°N. This implies that there are differences in average sea surface temperatures resulting from differences in insolation as can be seen in Fig. 1(a). In the first fifty metres the annual average of temperature ranges from <14°C in the Northern Adriatic to >21°C along the Israeli coasts (MODB Med5 data set, Brasseur, Beckers, Brankart & Shoenauen, 1996). In the same layer salinity reflects the direct influence of Atlantic water along the African coast, while a haline barrier is created in the eastern basin (Fig. 1(b)). These different environmental conditions obviously affect the distributions of biological populations in the two sub-basins, which are characterised by a high percentage of endemism (Sarà, 1985). Biodiversity is high in the Western

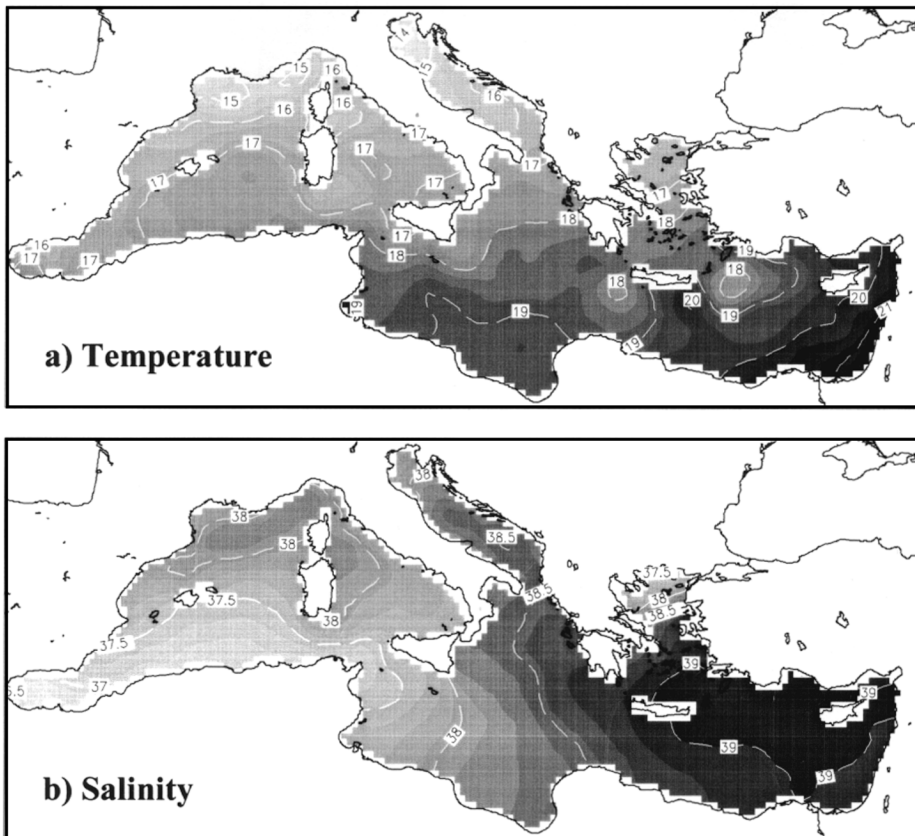


Fig. 1. Climatological distribution of (a) temperature and (b) salinity integrated over the upper 50 m. Data derived from MODB Med5 Data Set.

Mediterranean, but relatively impoverished in the Eastern Mediterranean (Por, 1978). This climatological pattern needs to be treated with care because the whole ecosystem is highly variable on interannual and longer time scales. These variations occur in terms of hydrodynamics (Roether et al., 1996), biochemical budgets (Malanotte-Rizzoli et al., 1997; Bethoux, Morin, Madec & Gentili, 1992) and in community composition (lessepsian migration, *Caulerpa taxifolia* invasive proliferation).

This variability and the relatively fast response (compared to open ocean) of the Mediterranean Sea to external conditions, suggest that physical/ecological interactions at the basin scale may have a profound influence in determining the evolution of the ecosystem. Further insight into these interactions may help in understanding the origins of this variability (i.e. ‘natural’ versus ‘man-driven’). Conversely, the specificity of the Mediterranean prevents a straight extrapolation of the results of the studies of variability to the global scale (and vice-versa), even if the majority of dynamic processes are present in the Mediterranean.

3. Eco-hydrodynamic interactions in coupled models

The formulation for a generic passive tracer Θ_i of an advection/diffusion equation in Reynolds averaged form is (Davis, 1994)

$$\frac{\partial \Theta_i}{\partial t} = -\mathbf{U} \cdot \nabla \Theta_i + \nabla \cdot [k \nabla \Theta_i - \langle \mathbf{u}' \theta'_i \rangle] \quad (1)$$

Where the velocity \mathbf{u} and the tracer θ_i are split into the average components \mathbf{U} and Θ_i and the statistically distributed zero-average fluctuations \mathbf{u}' and θ'_i where $\langle \rangle$ indicates the ensemble average. In nature, ensemble realizations of the same experiment are not possible so, exploiting a not always plausible ergodicity hypothesis, the ensemble operator is normally substituted by a time operator.

The generic biogeochemical tracer is assumed to be active in the sense that it is subjected to internal dynamics formally represented in a supplementary term, the reactor term q , added to Eq. (1). On the other hand a simplified hypothesis of no influence in the state equation of seawater is assumed. For sake of completeness, the reactor is expected to include the (not identically null) contributions to the evolution equation of the entire vector $\boldsymbol{\theta}$ of the biological state variables describing the system as well as the explicit dependencies on physical state variables and forcing, such as temperature T and irradiance I . Thus Eq. (1) can be extended to an active tracer as follows (Hofmann & Wroblewski, 1989):

$$\frac{\partial \Theta_i}{\partial t} = -\mathbf{U} \cdot \nabla \Theta_i = \nabla \cdot [k \nabla \Theta_i - \langle \mathbf{u}' \theta'_i \rangle] + q(\boldsymbol{\Theta} + \boldsymbol{\theta}', \bar{r} + T', I + I', \dots) \quad (2)$$

Which is usually simplified in

$$\frac{\partial \Theta_i}{\partial t} = -\mathbf{U} \cdot \nabla \Theta_i = \nabla \cdot [k \nabla \Theta_i - \langle \mathbf{u}' \theta'_i \rangle] + q(\boldsymbol{\Theta}, T', \bar{I}, \dots) \quad (3)$$

In the above equation the reactor q includes the internal fluxes within the single parcel of water plus all the sources and sinks expressed in terms of the averaged component state variables. To be strictly true, this widely shared assumption implies as a sufficient condition for reactor term to be linear in θ , T , I , in order to ensure the commutability of the average operator with q . This hypothesis implies a crude approximation of the real biological processes, which are intrinsically highly non-linear (Ulanowicz & Platt, 1985). In this way terms derived by the non-linear coupling both between averaged variables and higher order moments $\langle\theta_i\theta_j\rangle$ are disregarded. More accurate higher order closures are currently studied in theoretical ecology (Levin, Grenfeld, Hastings & Perelson, 1997; Bolker, Pacala & Levin, 1997) but at present no application has been attempted for marine environment. Alternatively, another justification can be invoked, assuming that all the state variables included in a model are representative of large, functionally equivalent communities and in this sense are themselves ensemble averages. Indeed, parameterisations are deduced from experimental measurements, which are performed on groups of individuals and represent the response to environmental conditions of populations, rather than individuals, so embedding the averaging operation. For this reason, attention must be paid in shifting from individual based models to population based ones. To express Eq. (3) as a function of averaged quantities only, the eddy transport divergence $\nabla\cdot\langle\mathbf{u}'\theta_i'\rangle$ is parameterised by analogy with the Reynolds stress approximation (Tritton, 1988) provided that the average process is carried out within a time window long enough to discriminate vertical vs horizontal diffusivity scales (Nihoul & Djenidi, 1987):

$$-\nabla\cdot\langle\mathbf{u}'\theta_i'\rangle\cong\frac{\partial}{\partial z}\left[K_v\frac{\partial\Theta}{\partial z}\right]+K_h\nabla_H^2\Theta_i \quad (4)$$

Where ∇_H is the horizontal gradient, and K_v and K_h are the horizontal and vertical eddy diffusivities. This parameterisation introduces the effect of the eddy transport on the tracer mean evolution and is correctly represented when the tracer and velocity fluctuations are correlated. This introduces a constraint on coupling biological and physical time scales: if θ_i' is assumed to be slowly varying in comparison with \mathbf{u}' this implies that the spectral windows as defined by Nihoul and Djenidi (1998) are different and the final contribution of the averaged term practically vanishes:

$$\langle\mathbf{u}'\theta_i'\rangle\cong\theta_i' \quad \langle\mathbf{u}'\rangle=0 \quad \text{if } \theta_i'\cong\text{const} \quad (5)$$

Conversely if the parameterisation proposed in Eq. (4) is used, the result obtained in Eq. (5) is no longer automatically true because only the averaged gradients present on the right hand side of Eq. (4) are considered. As a side issue, this suggests great care must be taken in coupling dynamical and biological tracers when the scales are different.

Introducing Eq. (4) in Eq. (3) the evolution of the state variable vector θ can be rewritten completely in terms of its averaged values Θ . If the effects of possible negative buoyancy on Θ_i are assumed to determine an additional vertical flux, Eq. (3) can be also extended to include the biologically mediated vertical transport:

$$\frac{\partial \Theta_i}{\partial t} = -\mathbf{U} \cdot \nabla \Theta_i + k_h \nabla_H^2 \Theta_i + \frac{\partial}{\partial z} \left[K_v \frac{\partial \Theta_i}{\partial z} \right] + w_{si} \frac{\partial \Theta_i}{\partial z} + q(\Theta, \bar{T}, \bar{I}, \dots) \quad (6)$$

Where w_{si} is the (negative) downward velocity associated to Θ_i .

The contribution to the time rate of change of Θ_i as a result of the physical forcing can thus be grouped in two terms:

- an *endogenous* sensitivity of the biological term to the forcing, such as that induced by temperature in the metabolic activity of primary and secondary producers
- an *exogenous* dependence that takes into account the modification in Θ_i concentration due to transport processes.

3.1. Coupled eco-hydrodynamic models in the Mediterranean Sea

All ecological models need information on the physical structure and dynamics of the marine environment and often simplifications of Eq. (6) are made by assuming idealised physical conditions. At the highest level of idealisation are conceptualizations that assume vertical and horizontal homogeneity. Examples include, bio-optical models (Morel & André, 1991; Antoine, Morel & André, 1995), that are designed to estimate Mediterranean primary production from CZCS satellite images, and ecological models set within a homogeneous mixed layer constant in time (Andersen & Nival, 1988). In such a class of models the endogenous dependence is the only non-vanishing term of Eq. (6), which can be rewritten as:

$$\frac{\partial \Theta_i}{\partial t} = q(\Theta, \bar{T}, \bar{I}, \dots) \quad (7)$$

These classes of model are usually referred to as 0D models, but this in reality is simplification which can be safely assumed only in particular situations such tank experiments or for short time intervals.

If, instead, only lateral homogeneity is assumed, a one-dimensional formulation can be obtained from Eq. (6)

$$\frac{\partial \Theta_i}{\partial t} = \frac{\partial}{\partial z} \left[K_v \frac{\partial \Theta_i}{\partial z} \right] + w_{si} \frac{\partial \Theta_i}{\partial z} + q(\Theta, \bar{T}, \bar{I}, \dots) \quad (8)$$

One-dimensional models are frequently found in literature, because vertical processes usually have the strongest signal. But they cannot account for lateral advection, eddy diffusion and other processes which are intrinsically three-dimensional. Table 1 summarises the main characteristics of a number of the ecological models that refer to the Mediterranean Sea. It lists many examples of 1D models including some that stress the influence of vertical turbulence on primary production (Zakardjian & Prieur, 1994), the influence of turbulent entrainment as a major source of nutrient input in Western Mediterranean (Klein & Coste, 1984), the influence of physical forcing on

Table 1
Classification of Eco-hydrodynamic models that have been developed for the Mediterranean Sea^a

Authors	Dim	Area	Temporal scale	Spatial Physical scale	Biological submodel				Coupling				Objective			
					Prod I	Prod. II	Nutr	Det/Doc	Bact	DO	T	L		Nutr	Turb	
Morel & André, 1991	0D	West Med	Year	Basin	–	–	–	–	–	–	–	–	–	–	Pr. Prod. From CZCS	
Antoine et al., 1995	0D	East Med	Year	Basin	–	–	–	–	–	–	–	–	–	–	Pr. Prod. From CZCS	
Béthoux et al., 1992	Box	Med Sea	Asymptotic	Basin	box	–	–	N,P	–	–	–	–	–	–	Nutrient Balances	
Sarmiento et al., 1988	Box	Med Sea	Asymptotic	Basin	Box	–	–	P	–	–	–	–	–	–	Nutrient Balances & Anoxia	
Klein & Coste, 1984	1D	NW Med	Days	50 m	Mellor Yamada 2	–	–	Nutr	–	–	–	–	Nutr	–	Influence as passive wind nut.	
Varela et al., 1992	1D	NW Med	Days	200 m	Mellor Yamada 2	2	1	Nrid Nox	–	–	T	L	Nutr	–	Influence forcings on DCM	
Zakarczjan & Prieur, 1994	1D	West Med	months	200m	–	1	1	Nrid Nox	–	–	–	L	Nutr	Turb.	Influence of turbulence	
Allen et al., 1998	1D	Adriatic	year	200 m	Mellor Yamada 2	E	R	S	E	M	T	L	Nutr	–	Ecosystem Study Calibrated.	
Tousseau et al., 1997	1D	Ligurian Sea	Year	200 m	Thermal	2	–	Nrid Nox (physiological)	DetSi Dom1 (mono) Dom2 (poly)	Bac	–	T	L	Nutr	–	Used as Bound. Condition for 3D Simulations.

(continued on next page)

Table 1
continued

Authors	Dim	Area	Temporal scale	Spatial Physical scale submodel	Biological submodel		Coupling					Objective			
					Prod I	Prod. II	Nutr	Det/Doc	Bact	DO	T		L	Nutr	Turb
Levy et al., 1998	1D	Ligurian Sea	Year	100m Box	1	2	Nrid Nox	Doms Doms Dets Detl	Bac	–	T	L	Nut	–	Fluxes Eval.
Solidoro et al., 1998	1D	Tyrrhenian Sea	year	100 m diffusive	2	1	Nrid Nox PO4	DetN DetP DetC	–	DO	T	L	Nut	–	Sensitivity analysis
Napolitano et al., 1999	1D	Ionian, Rhodus Gyre	year	200 m Mellor Yamada 2.5	1	1	Nrid Nox	Det	–	–	T	L	Nut	–	Ecosystem study
Pinazo et al., 1996	3D	Gulf of Lions	20 days	250 Km Mellor Yamada 2.5	1	–	Nrid Nox	DetN DetC	–	DO	T	L	Nut	–	Influence forcing and nut. Cycle
Civitarese et al., 1996	3D	Ionian Sea	Year	200 Km MOM	1	–	N	D	–	–	T	L	Nut	–	Nutrient balance
Tusseau et al., 1998	3D	Gulf of Lions	Year	200 Km General Circulat.	2	–	Nrid Nox Si	DetSi Dom1 (mono) Dom2 (poly)	Bac	–	T	L	Nut	–	Fluxes Eval.
Bergamasco et al., 1998	3D	North Adriatic	months	100 Km POM (nesting off line)	1	–	N	–	–	DO	T	L	Nut	–	Fluxes, nesting, influence
Zavatarelli et al., in press	3D	Adriatic	year	800 Km POM (MY 2.5)	ERSEM	–	–	–	–	–	–	–	–	–	biology Ecosystem study
Crise et al., 1998;	3D	Mediterranean	years	basin MOM	1	–	N	DetN	–	–	T	L	Nut	–	Ecosystem study
Crispi et al., 1999	3D	Mediterranean	years	basin MOM	2	1	Nrid Nox PO4	DetN DetP DetC	–	DO	T	L	Nut	–	Ecosystem study

^a N means Dissolved Inorganic Nitrogen, P Dissolved Nitrogen Phosphorus, Nut is a generic Nutrient, Nrid and Nox nitrogen in its reduced and oxidised form, Detx is the detritus expressed in different forms according with the value of x, ERSEM is the acronym of European Regional Seas Ecosystem Model, DO stands for Dissolved Oxygen.

the development and the evolution of Deep Chlorophyll Maximum (Varela, Cruzado, Tintoré & Garcia-Ladona, 1992), and that address sensitivity analysis and parameter identifiability related issues (Solidoro, Crise, Crispi & Pastres, 1998). All of these models are not strictly dependent on a specific geographic characterisation and hence are not specific to the Mediterranean, but seek to elucidate the influence of a given parameter on some phenomena (processes oriented studies). There are other 1D models that deal either with short time or space scales, or with specific sites, at which advection is assumed to be of secondary importance, for example in the Ligurian Sea (Tusseau, Lancelot, Martin & Tassin, 1997; Levy, Memery & Andre, 1998) or the Rhodes Gyre (Napolitano, Oguz, Malanotte-Rizzoli & Sansone, 1999). Such models are aimed at reproducing the ecosystem dynamics more realistically.

Analogously, by releasing the constraint on horizontal homogeneity and retaining the vertical constraint in Eq. (6), one obtains a 2D model:

$$\frac{\partial \Theta_i}{\partial t} = -U \cdot \nabla \Theta_i + k_h \nabla_H^2 \Theta_i + q(\Theta, \bar{T}, \bar{I}, \dots) \quad (9)$$

Such models are, however, seldom used for ecological studies since the capability to discriminate the gradients of light and nutrient availability down the vertical profile of a water column is of great importance in simulating biological cycles. The exception is in shallow water, where strong tidal mixing generates vertical homogeneity. It is evident, therefore, that as all terms present in Eq. (6) implicitly or explicitly depend on physical forcing, thus dynamic processes can be coupled with biology in a more realistic way if a fully 3D simulation is adopted.

Fully three-dimensional models have been developed for larger, but still limited, areas, e.g. the Gulf of Lions (Tusseau, Mortier & Herbaut, 1998; Pinazo, Marsaleix, Millet, Estournel & Vehil, 1996), the Ionian Sea (Civitaresse, Crise, Crispi & Mosetti, 1996), the North West Adriatic Sea (Bergamasco, Carniel, Pastres & Pecenic, 1998) and the Adriatic Sea (Zavatarelli, Baretta, Baretta-Bekker, Pinardi, in press). One model presents a fully 3D conceptualization for the whole Mediterranean basin (Crise, Crispi & Mauri, 1998; Crispi, Crise & Solidoro, 1998; Crispi, Crise & Mauri, 1999).

Models differ from each other in the parameterisation of the reactor term Θ , \bar{T} , \bar{I} . Moreover, the spatial scale and resolution of the model set a constraint on the amount of detail that can be included in describing the biogeochemical cycles. Indeed, in the case of a 1D model, or local area 3D models, ecosystem structure can be more easily identified, implicitly accounting for typical time and space scales in the simplifications. When dealing with larger spatial scales, the potential value of defining a unique biological submodel suitable for the whole area will be a trade-off against needing a much less detailed conceptualization of the ecosystem features. An alternative is to implement several different biological submodels for the different bioprovinces. However, this imposes an a priori 'solution' for the differences between the sub-basins, which will severely bias the model response. This would also substantially increase the complexity of the system, conceptually, mathematically and numerically.

There are then, obviously, other reasons for the differences in the parameterisation

of the reactor term, which derive either from the different objectives of individual researchers, or from the inherent differences between the areas being analysed. Availability of observational and experimental information is a key consideration in choosing the parameterisation, since the more complex a model is, the larger the number of parameters estimates which will be required. As a consequence there is an increase in the required amount of experimental data and knowledge of the processes described.

The biological submodels presented in Table 1 may be classified according to their ecological complexity:

1. the very approximate biological conceptualization in which biogeochemical compartments are ultra-aggregated from a functional point of view such as the NPD model (Crise et al., 1998; Crispi et al., 1999), the NPO model (Bergamasco et al., 1988), and the box model, which considers only few variables (Béthoux, 1979; Sarmiento et al., 1988),
2. a majority of more complex, but still aggregated, formulations, that take into account a food chain up to the zooplankton and a remineralization path through a detritus chain, using a number of state variable ranging from 5 to 10 (Varela et al., 1992; Tusseau et al., 1997; Tusseau et al., 1998; Levy et al., 1998; Pinazo, Marsaleix, Millet, Estournel & Vehil, 1996; Napolitano et al., 1998; Solidoro et al., 1998),
3. the European Regional Seas Ecosystem Model (ERSEM) biological submodel (Baretta, Ebenhöh & Ruardij, 1995), which describes both the pelagic and benthic ecosystems and the coupling between them in terms of the significant biogeochemical processes affecting the flow of carbon, nitrogen, phosphorus and silicon.

Table 1 also reports a few examples of box models (Béthoux, 1979; Sarmiento et al., 1988) even though they represent a different approach with respect to the other ones reviewed here. Regular boxes approximate the domain of integration and flows at the interfaces are prescribed a priori, instead of being computed. Although they are frequently used because of the simplicity of resolving the transport, box models are not particularly suitable for ecological modelling. Their description of the influence of dynamics and light on the ecosystem is poor, unless the number of vertical and/or horizontal boxes is large enough (but then this converges, at least in terms of complexity toward a level/layer model). Nevertheless the box model-based studies included in Table 1 represent important attempts to quantify the balances of nutrient at a basin level, and historically they are recognised as important steps towards the comprehension of the Mediterranean Sea dynamics on a multidecadal time scale.

4. The influence of physical forcing on the DCM, oligotrophy and the seasonal cycle

In describing the oligotrophic conditions of the Mediterranean Sea, both surface and subsurface production need to be considered as both are subjected to periods of

mixing and stratification, with the consequent variability in nutrient concentrations and light intensity.

The common paradigm of extreme oligotrophic conditions for the Mediterranean, in particular in Eastern Mediterranean, seems to hold for the surface waters. In the surface layer, CZCS level 3 satellite images (as processed by Goddard Space Flight Centre) show a prominent seasonal variability in the whole basin. Production peaks occur in Winter along with maxima in the standing crop with values reaching >1.5 mgChl/m³ in the Western basin, particularly in areas where upwelling frequently occurs (Crispi et al., 1999). In the Eastern Mediterranean, winter conditions are characterised by a depth-integrated chlorophyll in the first 200 m ranging from 11.3 mg m⁻² in the Levantine to 48.9 in the Rhodes Gyre area with an average value of 22.9 mg m⁻² (Vidussi, pers. comm.). Values found near Rhodes area were similar to those those found at a station in Ligurian Sea during the same period (Fabiano, Zavatarelli & Palmero, 1984).

However, this paradigm needs to be reassessed on seasonal and spatial basis, taking into account the role of DCM. As inferred in Fig. 2 (drawn according to Crispi et al., 1999), the Deep-Chlorophyll Maximum (DCM) is almost ubiquitous in the Mediterranean and the deepest DCM is found in the more oligotrophic areas (Eastern

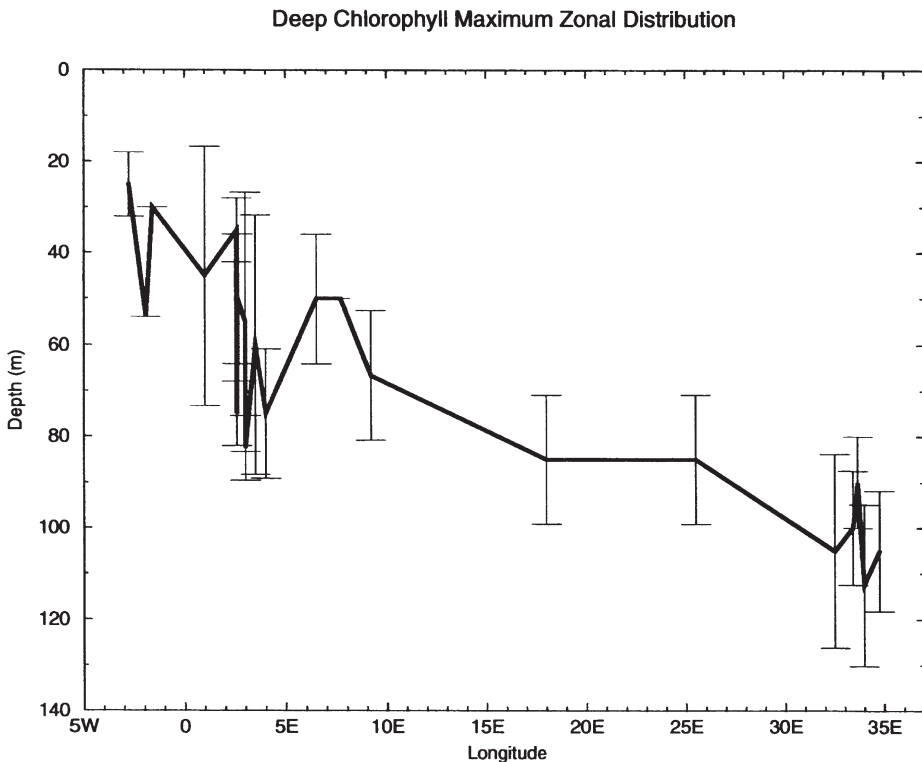


Fig. 2. Meridional averages of DCM depth as estimated from literature data.

Mediterranean), while in the North-west Mediterranean and Alboran Sea the DCM is far shallower and shows a clear seasonal oscillation in its depth. In open ocean the deepening of DCM is strictly connected with a concomitant increase of the water transparency, which is assumed to be an indicator of low standing crop in the surface layer. As expected, DCM depth closely follows the nutricline (Herbland, 1983).

This process, which is strongly influenced by phenomena occurring throughout the water column, should be addressed both by 1D and 3D models. In 3D models, biological details have to be kept to a minimum but horizontal effects can be taken into account, so enabling the analysis of the process within its geographical position within a basin. 1D models take account of the main forcing physical phenomena and permit finer ecological resolutions. In fact, in the marine environment the interplay between the exponentially decreasing Photosynthetic Active Ratio (PAR) of the solar radiation and the cumulative effects of nutrients limitation driven by entrainment/detrainment processes describe the typical vertical structure of biomass in the euphotic zone. On the other hand, intrinsically three-dimensional processes such as lateral advection, upwelling and eddy transport can profoundly modify simplified one-dimensional interpretations of primary production, which cannot intrinsically include lateral exchanges. This view is largely supported by a variety of discussions of DCM formation (Jamar, Winter, Banse, Anderson & Lam, 1977; Kiefer & Kremer, 1981; Estrada, 1985; Varela, Cruzado & Tintoré, 1994). Other mechanisms have also been proposed, such as differential grazing pressure (Hobson and Lorenzen, 1972) or varying sinking rate for phytoplankton (Takahashi & Hori, 1984). Taguchi, Ditullo and Laws (1988) explains DCM development as the result of variation in Chlorophyll:Carbon ratio, and so may not signal a biomass maximum.

In order to assess the influence of various biotic and abiotic factors on the, depth of formation and the magnitude of DCM, Varela et al. (1994) performed a numerical sensitivity analysis on a 1D coupled model (Varela et al., 1992). The transport component included both a vertically dependent eddy vertical diffusion term, based on k-model and a sinking term; the biological submodel structure reproduced the nitrogen cycle through nitrate, ammonium, two classes of primary producers and one heterotrophic pool (POM and zooplankton were estimated from other state variables, but not explicitly modelled). Model results show that the hypotheses of algal sinking or changes in the ch:ca ratio with depth do not determine the development of a DCM. Instead they stress the importance of optical and physical forcing, including self-shading effects, as well as the influence of the eddy diffusion transport both above, but even more importantly below, the nutricline. Biological mechanisms, including differential grazing pressure, and competition for nutrients between phytoplankton and bacteria, appear to affect the magnitude of the DCM, but not its depth.

More details on the role of biological processes might be provided by ecologically more detailed models, which would enable the carbon and nutrient cycling to be followed through a larger number of compartments and to elucidate, for instance, the competition between phytoplankton and bacteria for nutrients. Allen, Blackford and Radford (1998), by coupling the ERSEM model and a 1-D vertically resolved water column model for the southern Adriatic Sea, carried budget calculations out exploiting the model's results, which considered the roles of vertical mixing and in

situ nutrient cycling. Table 2 shows their results for annual and seasonal budgets for phosphate and nitrogen cycling in the euphotic zone. They were computed taking into account vertical mixing, net algal uptake, bacterial uptake and heterotrophic recycling. Nitrogen and phosphate are removed from the water column by phytoplankton and bacteria throughout the year. This demand is met primarily by the vertical diffusion of nutrients into the euphotic zone (80% of the biological phosphate demand; 75% of the biological nitrogen demand), while in situ recycling of nutrients via microzooplankton accounts for the balance. Two distinct ecological regimes may be identified. In winter and spring when the water column is strongly vertically mixed, phytoplankton dominates the system. Approximately 90% of the annual phytoplankton phosphate demand occurs at this time. In the summer and autumn when the water column is stratified, biological nutrient demand is much lower, bacterial phosphate demand exceeds that of phytoplankton and the net transport flux of nutrients is small. Bacteria are then out-competing the phytoplankton for phosphate, which may be the cause of the relatively low phosphate and chlorophyll-a concentrations in the surface layers of the model.

The time evolution of the vertical distribution of plankton density, as a result of the alternation of mixed and stratified conditions and of light seasonal evolution, appears with slightly different modalities along the Mediterranean Sea. Indeed, as it will be discussed later on, the well known permanent East–West, basin-wide, trophic gradients are the result of a coupling of these mainly vertical processes, with general circulation features, mainly horizontal, and with the biological mediated vertical flux of particulate organic material, sometimes referred to as biological pump. This has been illustrated using the 3D basin-wide MOM-NPD model. MOM-NPD is described in detail in Crise et al. (1998) and compared with data in Crispi et al. (1999). It is a primitive equation, general circulation model which discretizes the Mediterranean basin on a $\frac{1}{4}$ degree regular horizontal grid with 31 vertical levels. It is coupled to a biological submodel in which nitrogen flows are followed through the highly aggre-

Table 2

Annual and seasonal cycling of phosphate and dissolved inorganic nitrogen in the euphotic zone (top 100 m) at the southern site. Seasonal fluxes are in units of $\text{mmol m}^{-2} \text{quarter}^{-1}$ and annual fluxes in units of $\text{mmol m}^{-2} \text{yr}^{-1}$

	Spring	Summer	Autumn	Winter	Annual
Phosphate					
Phytoplankton uptake	-11.75	-4.48	-1.02	-0.76	-18.17
Bacterial uptake	-7.52	-5.78	-1.61	-1.03	-15.85
Heterotrophic recycling	0.158	4.62	1.57	1.15	7.58
Net transport	17.70	5.59	1.64	0.86	26.31
Nitrogen					
Phytoplankton uptake	-310.24	-124.90	-33.80	-29.36	-504.41
Bacterial uptake	-61.72	-72.54	-14.85	-1.47	-152.99
Heterotrophic recycling	2.31	110.29	31.00	28.55	173.86
Net transport	338.73	103.47	21.93	10.75	484.14

gated cycle composed of just three compartments, Dissolved Inorganic Nitrogen, Plankton and Detritus.

Two different scenarios are illustrated in Fig. 3. The first one is the January average for the period 1980–1986 using monthly mean wind stresses. The second is the

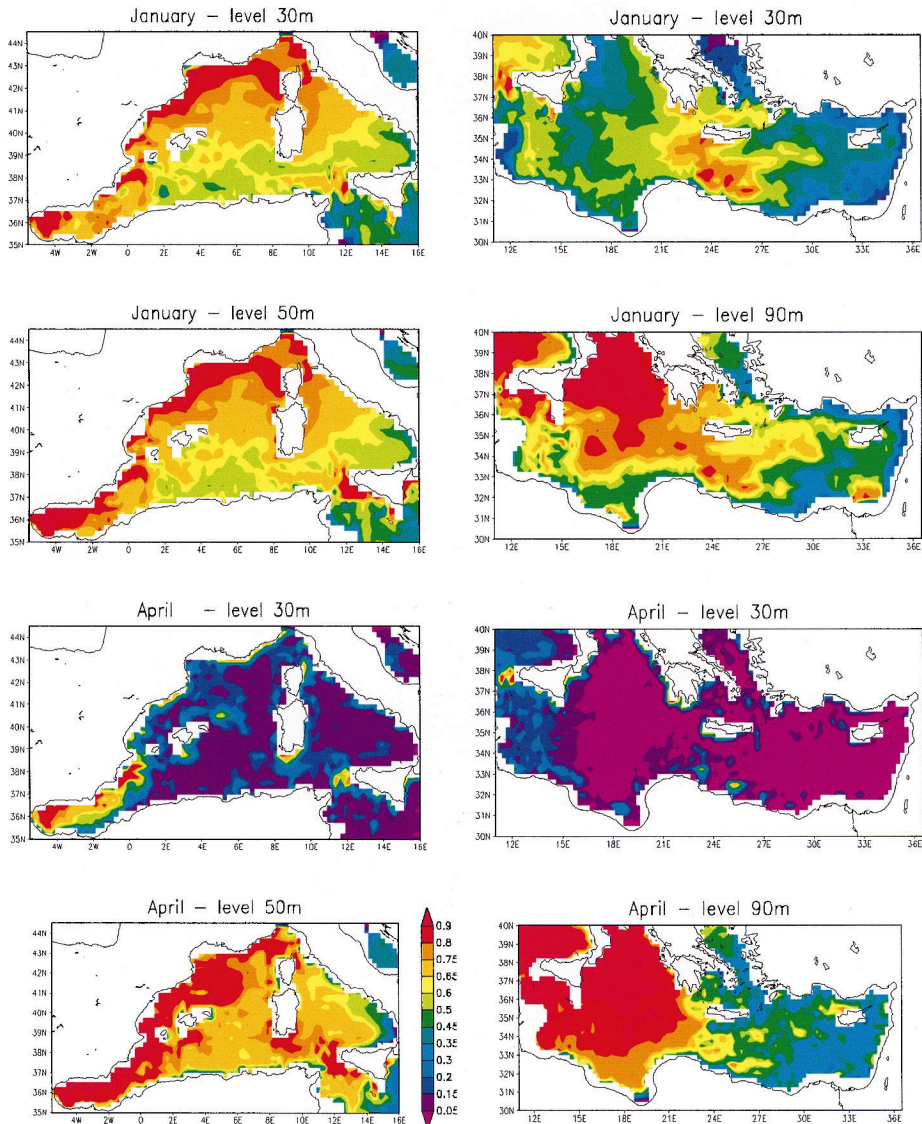


Fig. 3. Nitrates limitation index calculated according with Michaelis–Menten–Monod formulation in Western Mediterranean and Eastern Mediterranean at surface level (30 m for both subbasins) and in depth (50 m in Western Mediterranean and 90 m in the Eastern Mediterranean). The colour scale identifies in reddish the areas where the influence of nutrient limitation is low.

April average for the same period. The colour map shows the spatial variability of the classic Monod function. This is an index which varies from 0 to 1, which in the MOM-NPD is defined as the limitation of plankton growth by nutrient availability (the more reddish, the higher the index and the less the limitation). Two different reference levels are shown, one common to the whole basin (30 m) the other basin-specific (50 m in Western Mediterranean and 90 m Eastern Mediterranean) that approximates to the DCM depth of each sub-basin. As also shown by Varela et al. (1994), the DCM determines the nutricline depth, which is in turn related to light availability down the water column. In the Western Mediterranean, January conditions exhibit a well formed mixed layer: the two patterns relating to 30 m and 50 m are practically identical and nutrient limitation is having little influence on primary production in the northern sector of Western Mediterranean (Monod index higher than 0.75). Values are lower in the Algerian Basin but are still in excess of 0.5. In the Eastern Mediterranean there are large differences between the depth horizons at 30 m and 90 m and between the Ionian and Levantine basins. In the Ionian Sea and the Levantine Basin, surface waters contain low nitrates concentrations. The oligotrophy is relaxed in the Cretan Passage and in the area of the Rhodes Gyre. At 90 m nutrients virtually do not limit the growth either in the Ionian Sea or in large parts of the Eastern Mediterranean, but the mixing is not as deep as in the Western Mediterranean, since the Monod index patterns are not well related. Hence, at this depth, it is light limitation that plays the major role in keeping the phytoplankton biomass low at this season.

In April there is a clear difference in both basins between the upper and lower levels, because of the decoupling introduced by the onset of the seasonal pycnocline, that produces clearly oligotrophic conditions in the surface waters. The DCM then acts as a trap for nutrients, diffusing from below, so they do not reach the upper part of the water column. Hence we conclude that in the upper layer practically all the residual production is supported by rapid nutrient recycling.

A substantial relaxation in the severity of the oligotrophic conditions occurs in the lower layer in the North-Western Mediterranean, also local upwelling (visible at surface) occurs along the coasts of Sicily and Sardinia (Piccioni, Gabriele, Salusti & Zambianchi, 1988). Only in the eastern part of Eastern Mediterranean does there seem to be enough radiative energy to sustain primary production, and hence erode the available nitrogen pool. In summary, model results suggest that surface waters in the Western Mediterranean and in some areas of Eastern Mediterranean are not limited by nutrients in winter, but by PAR availability.

Numerical results from the MOM-NPD successfully reproduces the well known zonal skewness in the nutrient distribution, which is usually ascribed to the inverse estuarine circulation. Climatological distributions of nitrate (shaded) and velocity integrated over the first 200 m presented in Fig. 4 as obtained in a simulation forced with a 'perpetual year' NMC wind stress. The East–West nutrient gradient can best be illustrated by rearranging the nitrate concentration as shown in Fig. 5 in which the zonal distribution of simulated Dissolved Inorganic Nitrogen, integrated over the upper 200 m for 24 months is presented. The nutrient gradient is modulated by several perturbations that can be explained as the influence of the permanent gyres

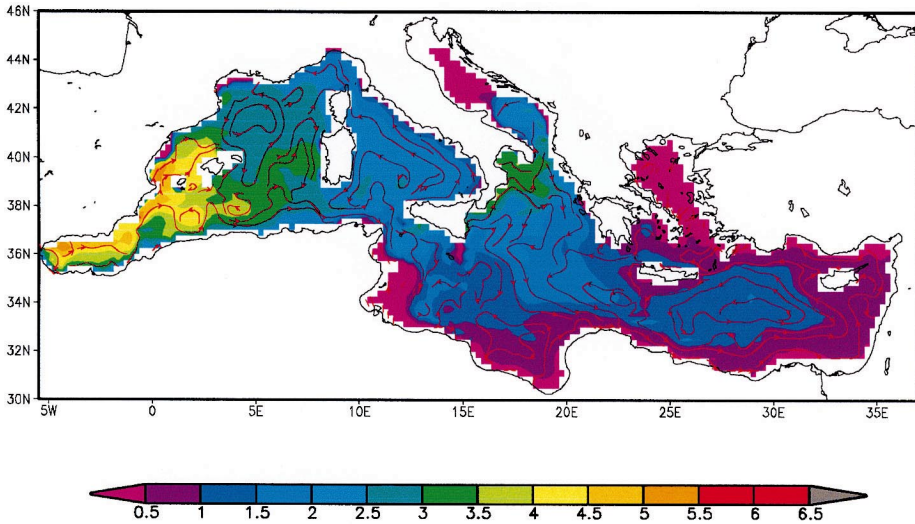


Fig. 4. Dissolved Inorganic Nitrogen (DIN) contained in the upper 200 m (shaded) with superimposed velocity streamlines averaged in the same layer.

on the nutrient distribution as demonstrated by (Crise et al., 1998). In the cyclonic areas the doming of isopycnals and the concomitant shoaling of the nutricline lead to higher nutrient availability in the surface layers while the opposite is true for anticyclones. Fig. 5 also shows reference estimates of nitrate, calculated as a meridional average (with 1° horizontal resolution) of the experimental data presented in Fig. 6 collected as in Fig. 7. The large standard deviations associated with experimental data can be explained by the seasonal variability inherent in the surface waters. Nevertheless the agreement with numerical results is good, and even where there is a mismatch (such as in the Ionian Sea and the Rhodes Gyre) the trend is still maintained.

In the model, the increasing eastward depletion is the result of the superposition of general circulation patterns, detrital fallout determined by biological activity and remineralization processes, as depicted in Fig. 8. The estuarine inverse circulation drives the nutrient-rich Atlantic water that flows in through the Gibraltar Strait eastwards in the surface layer of the Mediterranean Sea. Along this path, nutrients are assimilated by primary producers and transformed into detritus, which sinks out of the euphotic layer. This downward flux reduces the total amount of nutrients reaching Eastern Mediterranean at the same time, below the surface layer, Levantine Intermediate Water (LIW), that is richer in nutrients flows westward, and ultimately exits via the Gibraltar Strait. The LIW nutrient content increases as it spreads westwards, because of the mineralization of incoming detritus and mixing with the deep waters. The flux of detritus from the euphotic zone is responsible for the progressive depletion of nutrients from west to east. This enhances the trophic gradient that is produced by recirculation processes in the Mediterranean upper circulation. The comparison of two runs, differing only in sinking velocity (run b9 with $w_{si} = 1$ m/day

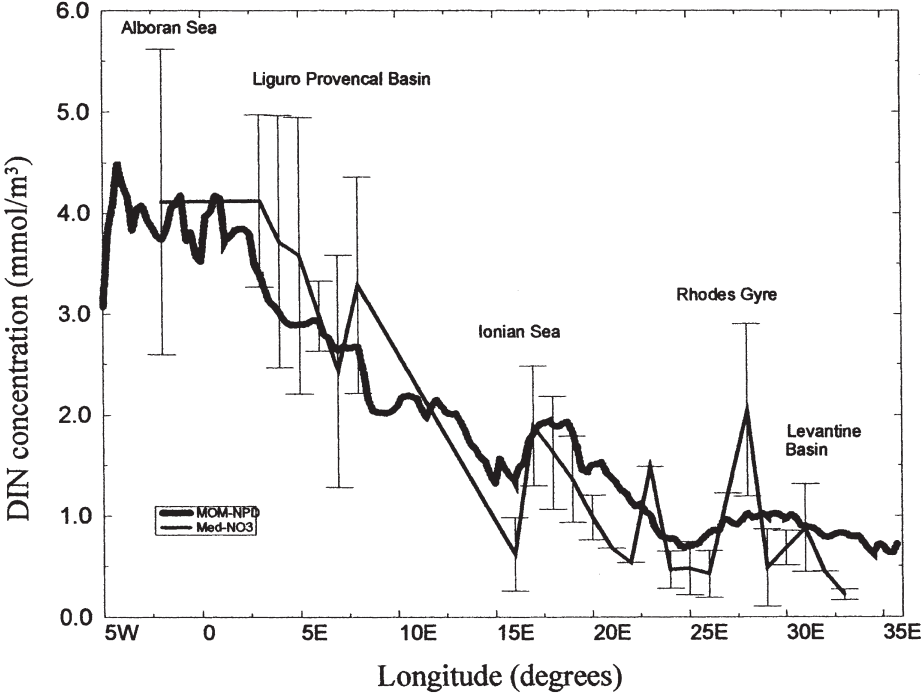


Fig. 5. DIN meridionally distribution averaged in the upper 200 m over 24 months(dotted line) and reference values obtained as meridional 1 degree means of measurements collected in the upper 200 m all over the basin. The large standard deviation in reference values also account for the seasonal cycle signal present in the measurements.

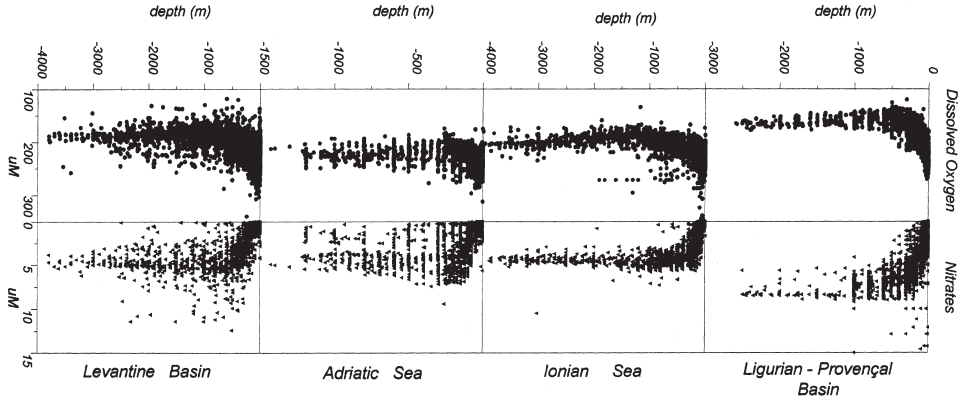


Fig. 6. Nitrates (black dots) profiles expressed in mMol/m^3 used in calculating the reference values zonally plotted in Fig. 3. All the stations pertain to pelagic waters (depth > 500 m). Oxygen consumption (DO in grey dots) below the euphotic zone is the signature of active remineralization as also evidenced by the concomitant nitrates increase.

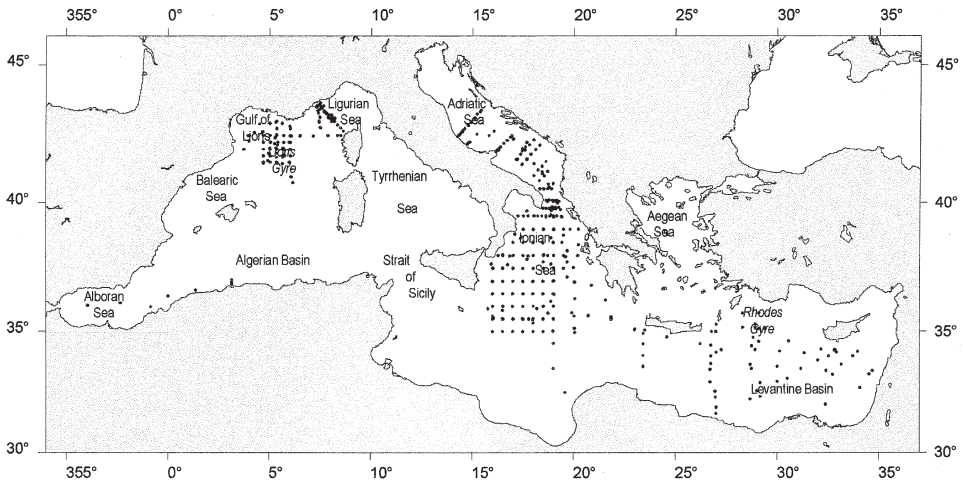


Fig. 7. Map of the positions of stations used to calculate the reference values shown in Fig. 3.

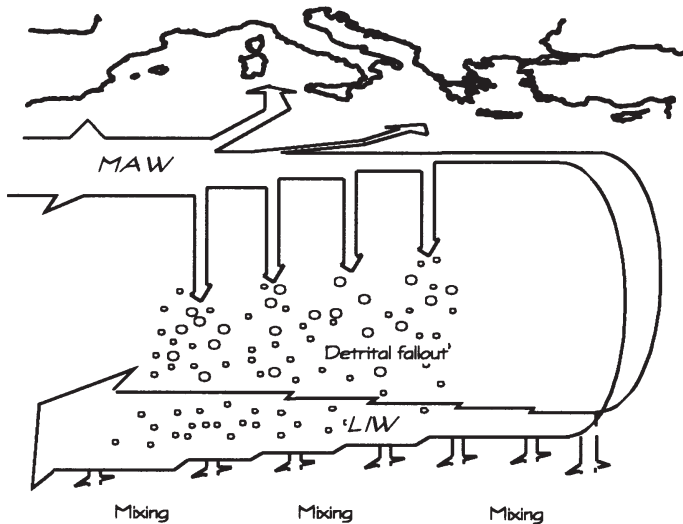


Fig. 8. Conceptual model of zonal trophic gradient formation.

versus run b10 with $w_{si} = 5$ m/day) strongly supports this interpretation. The zonal gradient is always present and constrained at the western side by the nutrient concentrations in MAW, but it is much steeper in the case of the run b10 (Fig. 9). To quantify the role of the vertical detrital flux, the meridional integral of the flux is computed by averaging between 30° and 44.5° over 24 months at 200 m depth and at 440 m:

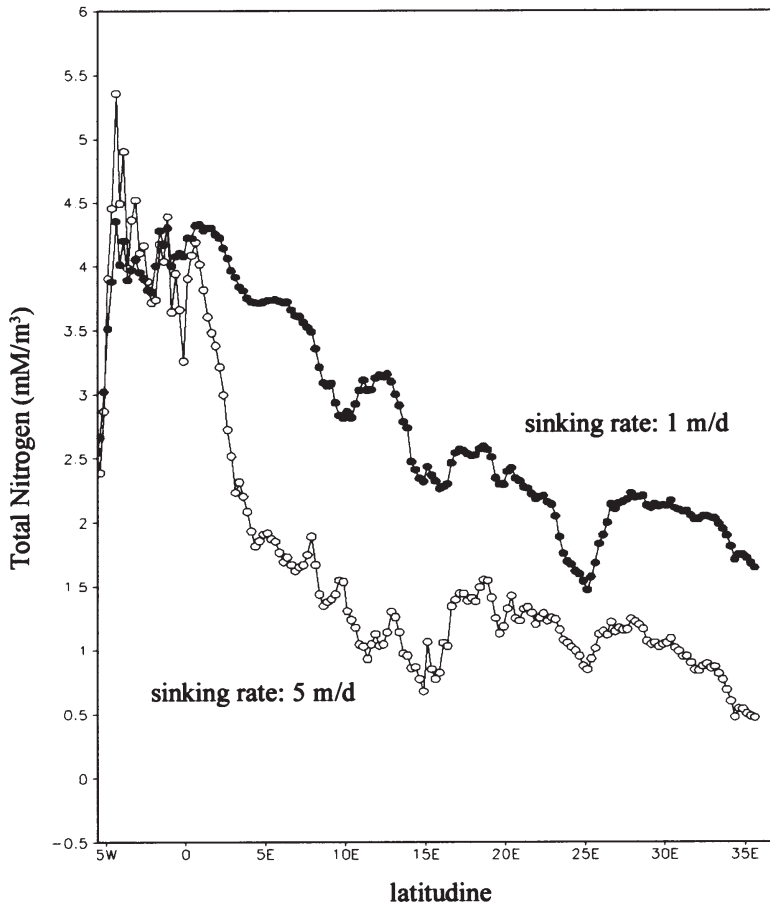


Fig. 9. Trophic gradient sensitivity to detrital sinking velocity. DIN meridional gradient estimated as in Fig. 3: run b9 has $w_{si} = 1$ m/day (full dots) while run b10 has $w_{si} = 5$ m/day (white dots).

$$Q_M(\phi) = \int_T \int_{30}^{44.5} w_{si} D_{Z=200} d\lambda dt \quad (10)$$

$$Q_L(\phi) = \int_T \int_{30}^{44.5} w_{si} D_{Z=440} d\lambda dt \quad (11)$$

$Q_M(\phi)$ is therefore the net loss of the upper layer as a result of vertical fluxes and a rough estimation of new production (Eppley & Peterson, 1979). The difference

between the downward flux of detritus Q_M and the losses below the nominal depth of the LIW Q_L (Fig. 10) gives an estimation of the LIW enrichment by remineralization processes. Indirect evidence of the relevance of remineralization is indicated by the dissolved oxygen profiles, which show a clear inverse correlation with nitrate profiles (Fig. 6).

The model suggests that thermohaline processes are modulated by wind-driven vorticity inputs that control the overall distribution of nutrients (nitrate can be assumed as a reliable proxy for the other nutrients at basin scale) as well as the spatial distribution assumed as combination of zonally and meridionally oriented processes.

5. Conclusions

The unique nature of the Mediterranean Sea has led to specific regionally targeted international multidisciplinary studies. Under the banner of these studies, a number of coupled eco-hydrodynamic models have been developed recently and are presented here; others are still under development. A number of the models refer to

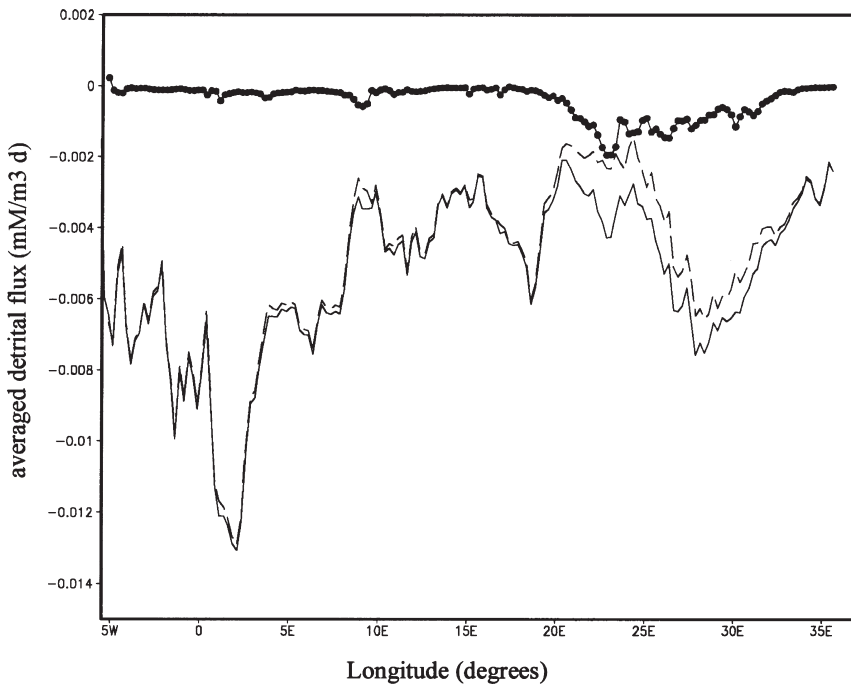


Fig. 10. Meridional averages of downward flux of detritus, Q_M (continuous line), and losses below the nominal depth of LIW, Q_L (dotted line), and $Q_M - Q_L$ (dashed line).

local and regional basins, some of which incorporate a highly detailed food web. Very few of them address the full basin with an aggregated description of the ecosystem. Using these numerical models, the importance of the physical forcing and its variability can be assessed. Simulation results stress the importance of general circulation processes in forming nutrient gradients, and the interplay between stratification and mixing, as modulated by the seasonal cycle of PAR on the trophic regime. The physical processes act as the interface between atmospheric variability and ecosystem response both in switching between a traditional food web and the microbial loop, and in determining the seasonal evolution of the Mediterranean oligotrophy at basin scale.

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