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Primary production in the northwestern Mediterranean*

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SUMMARY: The Mediterranean is, globally considered, an oligotrophic sea. However, in spite of its small extension, it presents considerable heterogeneity and, specially in the Western sub-basin, a number of hydrographic features contribute to increase its potential fertility. Phosphorus appears to be the most important limiting nutrient in the Mediterranean, although it is closely followed by nitrogen in this limiting role. The basic mechanisms of nutrient enrichment in the Mediterranean photic zone include vertical mixing in winter, coastal upwelling and the input of Atlantic waters through Gibraltar. River runoff is important, specially in the Western basin. One of the main causes of Mediterranean oligotrophy may be the water exchange at Gibraltar. The Mediterranean losses deep, relatively nutrient-rich water to the Atlantic through the Gibraltar Strait and receives an excess of superficial, nutrient-poor Atlantic water which compensates for the deep water outflow and the evaporation losses in the Mediterranean basin. However, the water flows at Gibraltar contribute to the fertility of the area through several mechanisms. One of them is due to the relatively shallow depth of the Gibraltar sill; in this zone, the entering waters become partially mixed with the richer outflowing waters and entrain additional nutrients into the Alboran Sea. Another enrichment mechanism is linked with the gyres induced by the Atlantic jet in the Alboran Sea and the associated upwelling near the coast of the Spanish side. Besides the general fertilization mechanisms mentioned above, the Western Mediterranean presents a series of mesoscale structures which represent sites of enhanced nutrient inputs to the photic layers. These structures include the shelf-slope fronts along the continental and insular coasts and the central divergence zones of the Liguro-Provençal and Catalano-Balearic Seas, which appear to be parts of a continuum. The relevance of some of these features for plankton production remained unrecognized until the last decades. In the vertical dimension, it has become apparent that the deep chlorophyll maxima, typical of the stratification season in the Mediterranean and other oligotrophic marine areas, are sites in which significant pulses of new production may take place, specially above the divergences, in which the nutrient-rich waters are closer to the surface. The occurrence of several mechanisms of fertilization, responding in different ways to environmental forcing, helps to enhance primary production levels throughout parts of the year including the stratification period. In the Catalan Sea, for example, the shelf/slope front and the central divergence located mid-way between the continental coast and the Balearic Islands appear to vary their relative contributions from spring to summer, with the divergence becoming more important later during the stratification period. The optimisation of sampling strategies linked to a better knowledge of the productive hydrographic structures and the improvement of methodology have lead to higher estimates of the primary production in the northwestern Mediterranean than where previously accepted. However, even with these increased estimates, the present level of total fish catches appears to be close to what could be the predicted limit according to some simple assumptions.

Key words: Primary production, fish catches, limiting nutrients, phosphorus, northwestern Mediterranean.

RESUMEN: PRODUCCIÓN PRIMARIA EN EL MEDITERRÁNEO NOROCCIDENTAL. – Considerado globalmente, el Mediterráneo es un mar oligotrófico. Sin embargo, a pesar de su pequeña extensión, posee una considerable heterogeneidad y, especialmente en la cuenca occidental, presenta estructuras hidrográficas que contribuyen a aumentar su fertilidad potencial. El fósforo parece ser el nutriente más frecuentemente limitante en el Mediterráneo, aunque seguido de cerca por el nitrógeno. Entreo los principales mecanismos de aporte de nutrientes a la zona fótica del Mediterráneo se encuentran la mezcla invernal de la columna de agua, los afloramientos inducidos por el viento en zonas costeras y la entrada de aguas superficiales atlánticas por Gibraltar. El aporte de los ríos es también importante, sobre todo en la cuenca occidental. Una de las principales causas de la oligotrofia del Mediterráneo es el intercambio de aguas en Gibraltar. El Mediterráneo pierde aguas profundas, relativamente ricas, que van hacia el Atlántico y recibe aguas superficiales del Atlántico, pobres en nutrientes, que compensan el flujo de salida de agua profunda y las pérdidas por evaporación en la cuenca mediterránea. Sin embargo, el trasiego de aguas en Gibraltar contribuye a la fertilización del sudo-

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este del Mediterráneo, por medio de diversos mecanismos. Debido a la escasa profundidad del Estrecho de Gibraltar, las aguas que entran se mezclan parcialmente con las aguas ricas que salen, lo que reintroduce una parte de los nutrientes en el Mar de Alborán. Por otra parte, los giros inducidos en el Mar de Alborán por la entrada de la corriente atlántica producen un afloramiento en la costa del lado español. Aparte de los mecanismos generales de fertilización citados más arriba, el Mediterráneo presenta una serie de estructuras de mesoescala que contribuyen de manera significativa a la entrada de nutrientes en la zona fótica. En la cuenca Noroccidental, estas estructuras incluyen los frentes y zonas de divergencia de los mares Liguro-Provenzal y Catalano-Balear. La importancia de algunas de estas zonas para la producción planctónica no ha sido adecuadamente reconocida hasta hace pocas décadas. En relación con la dimensión vertical de la columna de agua, se ha puesto de manifiesto que en el máximo profundo de clorofila, estructura típica de la época de estratificación en el Mediterráneo y otros mares oligotróficas, se producen importantes pulsos de producción primaria nueva. La magnitud de esta producción es particularmente importante en zonas de divergencia en las que las aguas ricas en nutrientes quedan relativamente cerca de la superficie. La aparición de mecanismos de enriquecimiento en nutrientes que responden de modo diferente a la variabilidad ambiental permite el mantenimiento de niveles de producción relativamente elevados durante diversas épocas del año. En el mar Catalán, el frente de plataforma-talud y la divergencia central situada entre la península y las islas Baleares contribuyen de modo variable a la fertilidad de la zona fótica; el frente de plataforma-talud parece ser más importante en primavera y la divergencia al final del período de estratificación. La optimización de estrategias de muestreo ligada a nuevas metodologías y un mejor conocimiento de las estructuras hidrográficas productivas, junto con el posible aumento del aporte de nutrients terrígenos, han permitido revisar al alza las estimaciones de la producción primaria en el Mediterráneo noroccidental. Sin embargo, un sencillo cálculo basado en valores de eficiencia ecológica considerados como típicos sugiere que las cifras actuales de captura pesquera se aproximan a la producción máxima sostenible.

Palabras clave: Producción primaria, capturas de peces, nutrientes limitantes, fósforo, Mediterráneo noroccidental.

INTRODUCTION

Primary production in aquatic ecosystems is related to the availability of external energy, which contributes to the injection of nutrients into the euphotic zone (Margalef, 1978). In turn, the magnitude of primary production sets an upper limit for the living resources that can be maintained in a given marine area. Spatial and temporal variance in the physico-chemical characteristics and biological components of the pelagic ecosystem modulates the transfer of this primary production to exploitable trophic levels (Cushing, 1982).

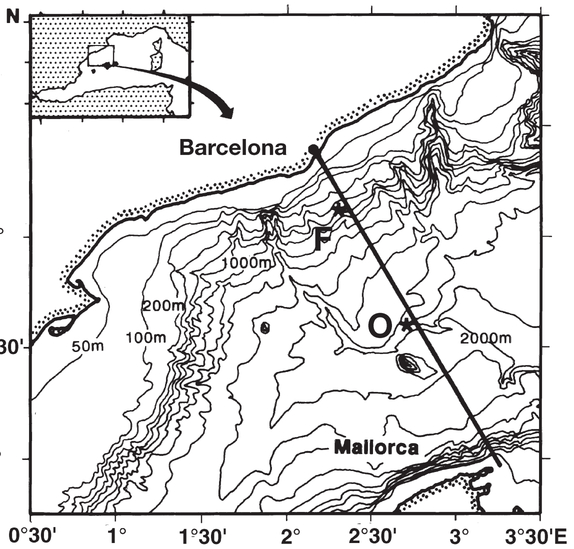

FIG. 1. – Bathymetry of the Catalano-Balearic Sea, between Barcelona and Mallorca. Position of the transect referred to in Figs. 2 and 3. The asterisks indicate the situation of the frontal (F) and divergence (O) stations referred to in Fig. 4.

The semi-enclosed character of the Mediterranean offers a good opportunity to explore global relationships between potential fertility and exploitable resources. Recently, improved resolution of oceanographic observations has underlined the importance of spatio-temporal hydrographic discontinuities in the transfers of energy through the Mediterranean food webs. With this background, the aim of this paper is twofold: To review some relevant data concerning the global fertility of the Mediterranean Sea, with emphasis on the western basin, and to present some results of research in the Catalano-Balearic Sea (Fig. 1), as an example of the role of mesoscale variability in shaping trophic relationships.

POTENTIAL FERTILITY AT A GLOBAL SCALE

In his review of the primary production data reported for the Mediterranean, obtained mostly in the western basin, Sournia (1973) found that yearly estimates converged between 80 and 90 g C m^{-2} year^{-1}. This regularity, qualified as "stupefying" by the author, occurred in spite of the heterogeneity of sources, sampling strategy and experimental methods. However, few data sets with systematic coverage, either temporal or spatial, were available at the time. Some years later, Béthoux (1981) used the UNEP (1977) data concerning terrestrial discharges of phosphorus and nitrogen in the Mediterranean Sea, along with his calculations of water fluxes, to estimate the potential fertility of the Mediterranean and its different basins (Table 1).

TABLE 1. – Primary production and new production estimates in the Mediterranean Sea.

Before 1980	Primary Production (g C m^{-2} y^{-1})	New Production (g C m^{-2} y^{-1})
Western Basin		35(3)-36(2)
North-western Basin		86(2)
Eastern Basin	6(2)-12(3)	11(4)
Mediterranean Sea	80-90(1)	16(2)-20(3)
Years 1980-1985		
Eastern Basin	109.4(6)	18(3)
western Basin	157.7(5,6)	52(3)
Mediterranean Sea	125(6)	

References: 1, Sournia (1973); 2, Béthoux (1981); 3, Béthoux (1989); 4, Dugdale and Wilkerson, 1988; 5, Morel and André, 1991; 6, Antoine *et al.*, 1995.

The consideration of phosphorus inputs to derive global estimates of potential fertility can be justified because this element appears to be the most important limiting nutrient in the Mediterranean (Margalef, 1963; Berland *et al.*, 1980), although it is closely followed by nitrogen in this limiting role. The average values given by Béthoux were 36 g C m^{-2} year^{-1} for the western basin and 16 g C m^{-2} year^{-1} for the whole Mediterranean. These figures represent "potential fertility" based on external nutrient inputs and amount to what is now generally denominated as "new production" (Dugdale and Goering, 1967). Total production, as measured experimentally, is the sum of "new production" and the so-called "recycled production", which is based on nutrient inputs originated from regeneration within the euphotic zone. More recent calculations using data on deep water fluxes and oxygen consumption (Béthoux, 1989) gave significantly higher values for the eastern basin (12 g C m^{-2} y^{-1}) and confirmed the previous estimates for the western basin (Table 1).

Based on CZCS data, Morel and André (1991) and Antoine *et al.* (1995) derived carbon fixation rates for different parts of the western and eastern Mediterranean, respectively. They used empirical relationships and pigment concentrations in the top layers to infer the vertically integrated pigment content in the water column. Primary production was estimated by means of a light-photosynthesis model which used integrated pigment content and additional information of temperature and photosynthetically available radiation. Table 1 gives the annual mean values calculated by these authors. Their predictions for the NW and SW regions of the studied area were compared with results from a limited set of field experiments; in general, there was good agreement. The annual carbon fixation rates for the western and eastern basins were respectively 158 and 109 g C m^{-2} year^{-1} (Antoine *et al.* 1995). These figures should be appraised in relationship with respective new production figures of 52 and 18 g C m^{-2} year^{-1}, calculated by Béthoux (1989) for the period 1980-1985, taking into account the increase in terrestrial P discharges due to recent anthropogenic activity. There is great uncertainty concerning the variability of the "*f* ratio", or ratio between new and total production in the Mediterranean (Béthoux, 1989; Minas *et al.*, 1988). Minas and Bonin (1988) derived a value of f= 0.36 from data corresponding to the winter-spring period, but considered that this figure was probably an underestimate for this part of the year. Using this factor, the total production for the western and eastern basins corresponding to the 1980-1985 potential fertility estimates would be 144 and 50 g C m^{-2} year^{-1}. The agreement with Antoine *et al.*, (1995) is fairly good for the western basin, but not for the eastern one. Curiously, as noted by Morel and André (1991), Mediterranean primary production figures lie relatively close to the mean annual fixation rates of 111 and 75 g C m^{-2} year^{-1} proposed for the world ocean by Bolin (1983) and Berger *et al.* (1987), respectively. This agrees with the view of the Mediterranean Sea as generally oligotrophic, but provided with a series of mechanisms enhancing fertility at certain times of the year or in connexion with more or less localized hydrographic structures (Morel and André, 1991; Estrada *et al.,* 1985). Some of these features will be discussed in the following sections.

GLOBALLY OPERATING ENRICHMENT MECHANISMS. SEASONAL MIXING AND EXCHANGE OF WATER WITH THE ATLANTIC

In winter, deep convection can occur in the Gulf of Lions and parts of the eastern Mediterranean (Medoc Group, 1970; Roether *et al.*, 1996; Schott *et al.*, 1996). Fluctuations in the intensity of this phenomenon have been related to interannual variations in primary production, partly because stronger mixing would incorporate deeper and richer waters and partly because deep water spreading would occur over a larger area (San Feliu and Muñoz, 1971).

Throughout the Mediterranean, winter cooling produces a breakdown of the thermocline and the ensuing vertical mixing brings nutrients from deep waters to the surface layers. In coastal waters, this phenomenon starts around November (Margalef and Castellví, 1967; Salat *et al*., 1978). Offshore data are more scarce and there may be strong interannual variability, as shown by the comparison of results from the few winter cruises carried out in the Catalano-Balearic Sea (Estrada and Margalef, 1988; Varela and Group FRONTS, 1991). Plankton blooms occur typically in winter-spring, when surface waters begin to stabilize, and in autumn, at the beginning of the mixing period (Margalef and Castellví, 1967; Estrada *et al*., 1985). The alternation of stratified and mixing periods confers strong seasonality to primary production, but the summer period is far from being as oligotrophic as often had been accepted. Limitation of vertical mixing over shallow depths and additional nutrient sources, such as coastal runoff, tend to make littoral areas more productive than open sea ones, although there may be exceptions (Cruzado *et al*., 1990).

The exchange of water at Gibraltar may be one of the causes of the low nutrient content of deep Mediterranean waters as compared with those of the Atlantic. Because of the overall excess of evaporation over precipitation, the Mediterranean functions as a negative estuary. Surface Atlantic waters, relatively nutrient-poor, enter through the Strait of Gibraltar, overcompensating for the evaporation losses, while deep Mediterranean waters flow into the Atlantic (Minas *et al.,* 1984). Béthoux (1981) estimated that the deep Mediterranean water flowing out of Gibraltar exported 443000 tons of phosphorus per year; this output would be balanced by runoff from land, entrance of phosphorus with the surface Atlantic water and atmospheric deposition (Dugdale and Wilkerson, 1988; Béthoux *et al*., 1992). In the case of nitrogen budgets, Béthoux *et al*. (1992) estimated that these sources were insufficient to compensate losses and proposed molecular nitrogen fixation by seagrass epiphytes and pelagic bacterioplankton species as a significant source of nitrate inputs.

MESOSCALE HYDROGRAPHIC FEATURES AND OTHER LOCALIZED SOURCES OF ENRICHMENT

The northern part of the western basin presents a cyclonic circulation wich extends from the Gulf of Genova to the Gulf of Valencia, across the Liguro-Provençal and Balearic basins. This feature is bound by shelf/slope fronts associated with the SW- flowing northern current on the continental side, and NE currents on the Corsican, Sardinian and Balearic Islands side (Prieur and Tiberti, 1984; Estrada and Margalef, 1988; Font *et al*., 1988). The central zone, marked by a doming of isotherms and isopycnals, has lower vertical stability than the margins and can be interpreted as a divergence. Both the shelf/slope fronts and the central dome or ridge-like structure play a key role in the fertility of this part of the Mediterranean.

Upwelling driven by strong NW winds (Mistral) is important in the Gulf of Lions, where the coastal profile is favourable (Minas, 1968). Wind driven upwelling may occur, in winter, in the Catalano-Levantine coast of Spain (Margalef and Castellví, 1967), but further research is neded in order to identify its importance.

Although the exchange at Gibraltar represents a global loss of nutrients from the Mediterranean, the inflow of Atlantic waters, and the resulting circulation patterns are associated with nutrient enrichment in the Southern basin. The responsible hydrographic features include: 1) turbulent mixing in the Straits, which drags nutrient from deep Mediterranean waters into the euphotic zone (Minas *et al*., 1984); 2) upwelling in the Alboran Sea and frontal zones (like the Almería-Orán front) associated with the anticyclonic gyres caused by the inflow of Atlantic water (Minas *et al.,* 1984; Lohrenz *et al*., 1988); and 3) the effects of the Atlantic current, which has a higher nutrient content than surface Mediterranean waters and presents strong dynamic activity along the Algerian coast, where meanders and eddies can produce points of enhanced phytoplankton growth (Taupier-Letage and Millot, 1988).

Land runoff is especially important in the northern zone, where rivers like the Rhône, flowing into the Ligurian Sea, the Po, flowing into the Tyrhenian and to a lesser extent the Ebre, running into the Catalan Sea, are important sources not only of contaminants, but also of phosphorus, nitrogen and other nutrients. Temporary discharges due to storms may produce intense local enrichment (Estrada, 1979), but their contribution is difficult to quantify. Béthoux (1981) estimated that phosphorus from terrestrial runoff accounted for 1/3 of the potential new production in the Ligurian and Tyrhenian Seas. Due to lower rainfall, the global contribution of land sources is much smaller in the southern part of the Mediterranean.

THE VERTICAL VARIABILITY OF PLANKTON BIOMASS

One of the most typical features of the phytoplankton distribution in the Mediterranean is the occurrence of a Deep Chlorophyll Maximum (DCM) during a large part of the year, when there is a certain degree of stratification of the water column, This DCM results from the accumulation of actively growing biomass and increased pigment content per cell due to photoacclimation (Estrada, 1985b). The contribution of these two factors varies throughout the year. The DCM occurs within the pycnocline (Fig. 2), at a depth in which nutrients become available and light, although generally of the order of 1% that at surface, is still sufficient for growth. The reduced diffusion losses at the pycnocline contribute to the maintenance of the biomass peak. The presence of the DCM accentuates the strong vertical differentiation of the pelagic ecosystem into a light- sufficient but nutrient-limited upper layer, based mainly on recycled production, and a nutrient sufficient but light-limited lower layer, where new production takes place (Herbland and Voituriez, 1979). These vertical patterns affect the structure of the trophic links among the diverse plankton components and are accompanied by changes in the relative importance of the microbial versus the classical, zooplankton-based, food web. In addition, sporadic enrichment events at the nutricline level may superimpose considerable horizontal patchiness on the elevated phytoplankton concentration background of the DCM (Estrada, 1985a; Latasa *et al*., 1992).

In spite of light limitation, primary production at the DCM may be significant. For example, in summer 1983, the phytoplankton of the DCM contributed up to 30% of the total primary production in the water column of the Catalano-Balearic Sea (Estrada, 1985a). The DCM cells are preyed upon by herbivorous zooplankton which, in turn, adjusts its migration patterns in relation to the distribution of food organisms (Alcaraz, 1988). In relation to consumers, the biomass accumulation at the DCM has not only quantitative, but also qualitative importance, because grazing efficiency is likely to be enhanced above a certain prey density threshold (Dagg, 1977; Saiz and Alcaraz, 1990). In addition, increased nutrient availability favours the growth of larger phytoplankton cells at the DCM than in the upper layers (Delgado *et al*., 1992); larger prey sizes may represent an advantage for certain zooplankton organisms.

COMPENSATION OF MECHANISMS. THE EXAMPLE OF THE CATALANO-BALEARIC SEA.

Superimposed on the seasonal cycle, which may present strong interannual differences, short-term changes in meteorological forcing and hydrographic heterogeneity interact to produce intermittent imputs of nutrient to the upper layers, through mechanisms such as instabilities at fronts or breaking of internal waves at the thermocline. These enrichment events originate pulses of phytoplankton growth which entrain a response of the other trophic levels. The result is a typically patchy distribution of phyto-and zooplankton, both in space and in time.

The diversity of mechanisms of fertilization and their spatio-temporal variability has the effect of maintaining relatively more stable primary production levels than would be possible otherwise. One example of this type of compensation can be found in the Catalano-Balearic Sea which, in recent decades, has been the subject of a series of multidisciplinary surveys aimed at the study of the coupling betwen physical forcing and biological fluxes (Estrada *et al*., 1993).

The Catalan and Balearic fronts follow, respectively, the shelf-break along the continental and the Balearic Islands sides of the Catalano-Balearic Sea, leaving a region of divergence (Fig. 2) or at least decreased stability in the central zone (Font, 1986; Estrada and Salat, 1989). These frontal structures appear to form a continuum with similar ones in the Liguro-Provençal basin and are associated with the prevailing current flows along the shelves (Estrada and Margalef, 1988). The main marker of the Catalan front is a salinity gradient enhanced by the influence of river runoff, while the Balearic front is mainly characterized by a temperature gradient. Both fronts may be affected by meanders and instabilities in the form of eddies or filaments (Millot, 1987; Wang *et al*., 1988). These instabilities, together with the ageostrophic cross-frontal circulation may contribute to local enrichment. Font (1986) suggested that interaction between meanders of the shelf-break fronts and the bottom topography could produce cyclonic eddies and upward motions which could originate fertilization events. The role of the central divergence as a zone of enhanced nutrient supply has been discussed by Estrada and Margalef (1988), who estimated that it could contribute up to 1/3 of the total production in a slice of the Catalano-Balearic Sea between the Catalan coast and 200 km offshore.

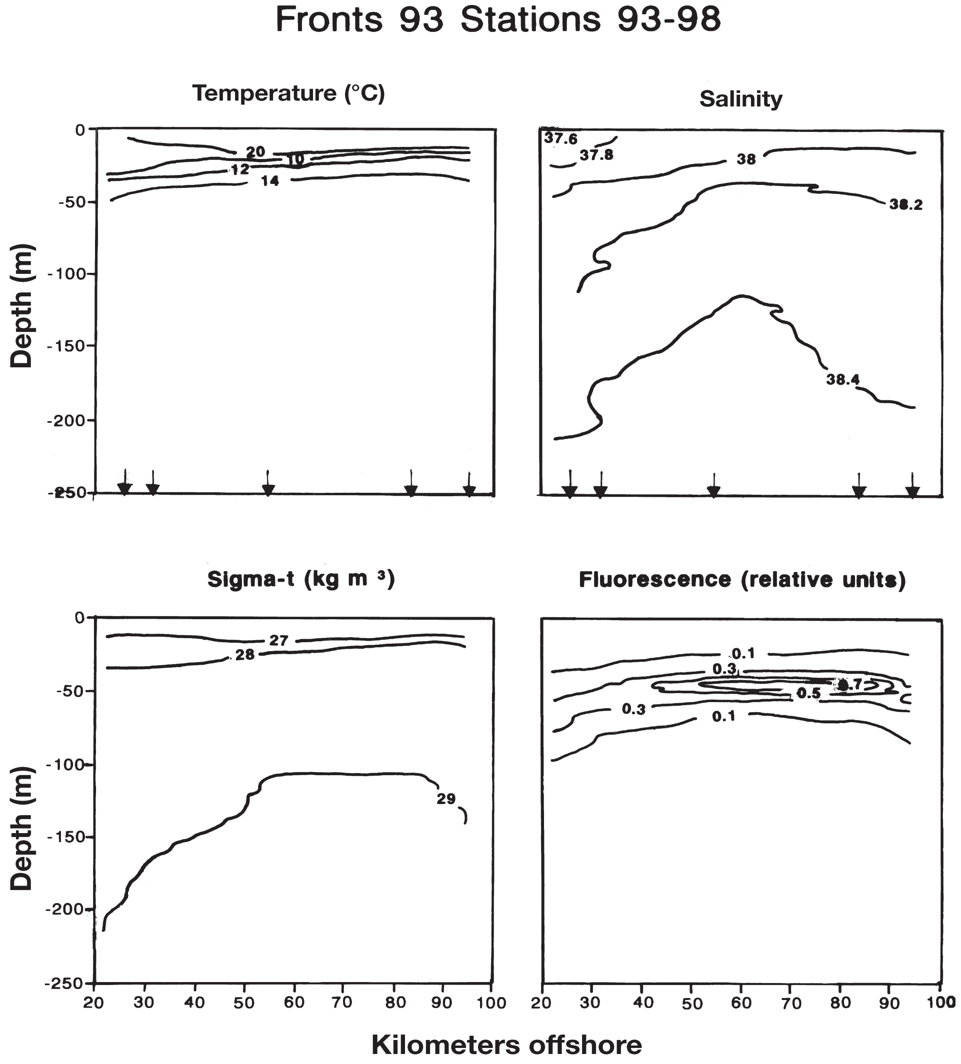

FIG. 2. – Distribution of temperature, salinity, sigma-t and fluorescence along the transect shown in Fig.1, during June 1993 (cruise FRONTS 93).

A graphic presentation of the integrated primary production data for a series of cruises carried out between July 1983 and February 1990, along a transect between Barcelona and the Balearic Islands is shown in figure 3. The limited coverage of the data does not allow calculation of yearly averages, but it can be seen that only a few measurements exceed 432 mg C m^{-2} d^{-1}, the average daily value corresponding to a total production of 158 mg C m^{-2} year^{-1}, the estimate given by Antoine *et al.* (1995) for the western Basin between 1980 and 1985 (Table 1). The highest C fixation rates were measured near the Catalan front, in May 1989, after a fertilization event, and in March 1985, during the winter-spring bloom. The small proportion of data obtained during this period could be an explanation for the generally low values of figure 3, in relationship with the estimates of Table 1. Apart

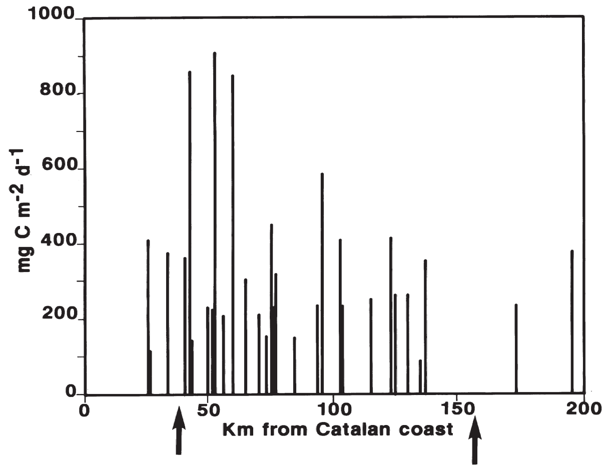

FIG. 3. – Spatial variability of primary production along the transect shown in Fig. 1. Data from cruises PEP 82, PEP 83, FRONTS-3-85, PEP 85, PEP 86, PEP87, FRONTS 89 AND FRONTS 90. Arrows indicate the 1000 m isobath.

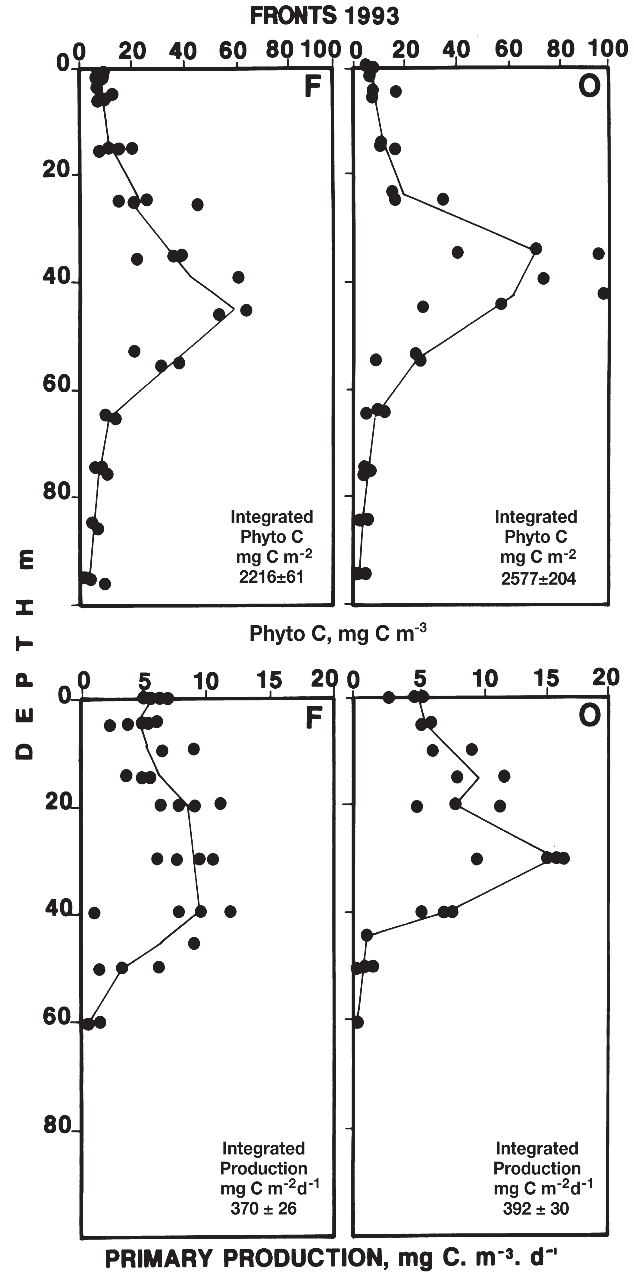

FIG. 4. – Vertical distribution of phytoplankton carbon (Phyto C, mg m^{-3}) and primary production during repeated samples of the frontal (F) and divergence (O) stations (Fig. 1), carried out in June 1993 (cruise FRONTS 93). The value for phytoplankton carbon was derived from chlorophyll a data, using a C/Chlorophyll a ratio = 50. The numbers within each graph indicate the mean values (± standard error of the mean) of phytoplankton C or primary production.

from the Catalan Front points, the central zone shows relatively high levels of production, even during the stratification period. As concluded by Alcaraz *et al.* (1994), maximum zooplankton biomass and metabolic activity tend to occur at the shelf/slope front, but this situation may be reversed in periods of strong stratification, as happened during June 1993. In this case, phytoplankton carbon and primary production were similar at the slope front and the central divergence (Fig. 4), and the highest activity of the classical food web was found at the divergence (Calbet *et al.*, 1996). A possible explanation is that, in the course of the warm season, the top layer of stratified waters becomes thicker and the nutricline deepens, so that instabilities at the frontal zone become unable to introduce nutrients into the upper layers. However, the nutricline continues to be relatively shallow in the central zone; thus, fertilization events at the nutricline level may still introduce significant amounts of nutrients into the euphotic zone. This may explain the detection, in mid-summer, of an enhanced chlorophyll signal in the central zone between the continent and the islands (image of August 1981 in Morel and André, 1991). The importance of the central divergence of the NW Mediterranean as a source of food for the consumer trophic levels affects not only zooplankton (Pinca and Dallot, 1995), but also large mammals such as the fin whale (*Balaenoptera physalus*), which has been found to concentrate in this region (Forcada *et al.*, 1996). These authors suggested that whales may feed on euphausiids like *Meganictyphanes norvegica*, which could be especially abundant in the divergence area; however, available information on the whale diet in the Mediterranean is scarce, and it would be very interesting to gather more data.

PRIMARY PRODUCTION AND POTENTIAL FISH CATCHES.

The Mediterranean Sea has been typically characterized by its oligotrophy. However, the low nutrient reserves contrast with moderate levels of primary production, an observation presented by Sournia (1973) as the “Mediterranean paradox”. The contradiction can be explained by the importance of regenerated production, by the supply of nutrients from the atmosphere and land runoff, and by the contribution of sporadic fertilization at hydrographic structures such as frontal zones.

Phytoplankton production is the main source of matter and energy for the other components of the food web. If inputs and outputs of materials in the pelagic ecosystem are considered to be in steady state over a reasonably long period, the amount of energy available for the upper trophic levels will be equivalent to new production, or production based on nutrient inputs from outside the euphotic zone. This quantity can be compared with the yield of exploitable living resources. Total combined fish and shellfish catches for 1993 were $1.670 * 10^9$ kg of wet weight (FAO, 1995), a figure only 50% higher than the 0.89 to $1.1 * 10^6$ kg recorded between 1963 and 1969 (Gulland, 1971), in spite of a presumably much higher increase in "fishing mortality". Assuming that 10% of these catches comes from the Black Sea (a rather low estimate, according to Gulland, 1971), the fish yield for the Mediterranean proper would be $1.503 * 10^6$ kg year $^{-1}$. Estimates of new production (or potential fertility) given by Béthoux (1981) for the whole Mediterranean are approximately 20 g C m^{-2} year^{-1} or $50 * 10^{12}$ g C year $^{-1}$ (Table 1). A large source of uncertainty in contrasting these figures with fish yields arises from the lack of precise information on ecological efficiencies and on the composition of the diet of exploitable fishes. Assuming a constant ecological transfer efficiency of 10% and a composition of the exploitable fish (scenario A) with 50% of first level and 50% of second level carnivorous fish (Russell-Hunter, 1971), the maximum potential fish catch would be about $3.3 * 10^9$ g of wet weight of organic matter per year. This is less than a factor of 2 from the reported catch, which is likely to be underestimated. However, the assumptions of scenario A are likely to be unrealistic for the Mediterranean, where a large part of the catch consists of clupeid fishes like sardine and anchovy. Another, more favourable scenario (B) could take into account the observation that sardine and anchovy, which constitute about 60% of catch in the Catalan coast (J. Lleonart, pers. comm.) may be able to feed also on phytoplankton. It is not clear what fraction of the diet could be contributed by phytoplankton (James, 1988; Bulgakova, 1993; Tudela and Palomera, 1995). For the sake of comparison it will be assumed that the contribution is 50%, a presumably high value (James, 1988), and that the other 50% is provided by herbivorous zooplankton. If the other 40% of exploitable fish follows the feeding patterns of scenario A, the maximum potential fish catch would be about $21 * 10^9$ kg of wet weight. Given that scenario A is rather pessimistic, but B appears too optimistic, it can be speculated that the actual figures of potential fish catch lie somewhere between those corresponding to A and B. The outcome would not change much if the possible recent increases in new production suggested by Béthoux (1989) are taken into account.

Similar considerations can be applied to the Catalan coast (Table 2). For simplicity, calculations have been referred to a band parallel to the coast, 400 km long and 27 km (15 nautical miles) wide, in which both primary production and fishing effort are assumed to be distributed homogeneously. Considering an average new production of 86 g C m^{-2} year^{-1} (the highest value from Table 1), and using the same approximations of scenario A for transfer

Table 2. – Catalano-Balearic Sea. Potential and reported fish catches.

1993 catch:	$5.48 * 10^7$ kg wet weight
Exploited area: 400 km long * 27 km wide =	$1.1 * 10^{10}$ m^2
New production (from Béthoux, 1981) $86 * C\ m^{-2}\ y^{-1} * 1{,}1\ 10^{10}\ m^2 =$	$95 * 10^{10}$ g C y^{-1}
Scenario A	
Carnivorous fish: 50% 3rd and 50% 4th trophic level	
50 % of available C at 3rd trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.01 * 0.5 =$	$0.47 * 10^{10}$ g C y^{-1}
50% of available C at 4th trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.001 * 0.5 =$	$0.047 * 10^{10}$ g C y^{-1}
Total potential fish catch:	$0.52 * 10^{10}$ g C y-1 or $6.3 * 10^7$ kg wet weight y^{-1}
Scenario B	
60% clupeid fish: 50% herbivorous and 50% carnivorous at 3rd trophic level	
60% * 50% of available C at 2nd trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.6 * 0.5 * 0.1 =$	$2.8 * 10^{10}$ g C y^{-1}
60% * 50% of available C at 3rd trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.6 * 0.5 * 0.01 =$	$0.28 * 10^{10}$ g C y^{-1}
40% other fish: 50% 3rd and 50% 4th trophic level	
40% * 50% of available C at 3rd trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.4 * 0.5 * 0.01 =$	$0.19 * 10^{10}$ g C y^{-1}
40% * 50% of available C at 4th trophic level: $95 * 10^{10}$ g C y^{-1} $* 0.4 * 0.5 * 0.001 =$	$0.019 * 10^{10}$ g C y^{-1}
Total potential fish catch:	$3.3 * 10^{10}$ g C y^{-1} or $39 * 10^7$ kg wet weight y^{-1}

efficiency and the composition of the fish catch, the maximum fish production would be 6.3 * 10^7 kg of wet weight year^{-1}, practically the same as the present fish catch (data from J. Lleonart, pers. comm.). This close coincidence is likely to be fortuitous, given all the simplifying assumptions. In the case of scenario B, the maximum fish production would be 39 * 10^7 kg of wet weight year^{-1}, about seven times the actual catch. Taking into account the assumptions of scenario B, that implying a short food chain for a large part of the exploitable fish appear overoptimistic, the main conclusion from this calculation exercise is that the present catch is fairly close to the potential one. Another point to consider is that commercial fish catches are accompanied by an important amount of discarded fish, which goes unrecorded.

A question which can be linked to the "paradox of the Mediterranean" concerns the apparently high yield of Mediterranean fisheries, in relation with relatively low primary production values. Cushing (1975) observed that the transfer coefficients from primary and secondary production decreased with increasing primary production, so that oligotrophic areas could be more efficient that highly productive regions. The observations of Alcaraz *et al.* (1985), who reported than the ratio between zooplankton and phytoplankton biomass was higher in the western Mediterranean than in the NW African upwelling region, suggest a relatively high ecological efficiency in the Mediterranean.

The calculations presented above are only a very rough approximation. Further research is needed on the link between primary production, the structure of food webs and production at the level of available resources. It appears however, that fish resources in the NW Mediterranean are already sustaining high exploitation levels. Economic progress in the fishery should come from improved ecological and economic management, rather than from increased total catches.

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