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The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral

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Abstract

The Mediterranean climate exerts a major influence on the basic properties of the Mediterranean Sea, which constrains the structure and dynamics of the ecosystem. Seasonal variations in the marine climate follow the expected unimodal seasonality only for temperature, while most other forcing factors show a complex variance structure, with dominant time scales of 50–100 days (e.g. wave action), and with some of the factors acting as random factors ('white noise') at the annual scale (e.g. rainfall), thereby limiting the predictability of the system. The resulting ecosystem seasonality is unconventional and poorly linked to temperature. The prolonged period of high atmospheric pressure and associated high irradiance and calm waters in late winter is the main seasonal trigger in the NW Mediterranean Sea, setting the development of a phytoplankton bloom, as well as the recruitment of the benthos. Decadal changes in the Mediterranean marine climate are characterized by the dominance of oscillations with a 22-year period, suggesting an important solar forcing on the climate. This forcing masks the monotonous trends, such as the warming and increased sea level in the Mediterranean, expected from anthropogenic forcing. Records of decadal changes in the ecosystem often display a monotonous trend in the deterioration of water quality, indicative of human effects as the main forcing agent, while climatic forcing, which displays oscillatory variation, is of secondary importance. The paucity of long-term records precludes a robust analysis of ecosystem response to decadal climatic forcing. This absence can be partially remediated by the ability to interrogate the long-lived organisms that represent an important, albeit endangered compo-

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ment of Mediterranean biodiversity, to extract records (e.g. growth, temperature, changes in the nature of the dissolved inorganic carbon pool) of the changes they have witnessed. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Mediterranean climate, characterized by warm, dry summers and mild, humid winters, is so distinct that the term ‘Mediterranean climate’ is now used as a generic term to characterize similar climate regimes elsewhere, as for example in California, Australia, and Chile (Strahler, 1981). The environmental conditions imposed by this climate have resulted in the development of a similarly distinct vegetation, the Mediterranean vegetation, sharing similar traits across the widely distant regions under Mediterranean climatic regimes (Strahler, 1981). Hence, the Mediterranean climate acts as a template shaping terrestrial ecosystem structure. Whether this interaction between climate and ecosystem structure and dynamics also applies to the marine environment has not, however, received direct attention, despite the fact that the documented study of the dynamics and ecology of the Mediterranean Sea predates those of other marine basins in the western world by at least a millennium (e.g. Peterson, Stramma & Kortum, 1996).

The marine climate of the Mediterranean Sea is distinct, and is characterized by relatively warm and salty, nutrient-poor waters. These characteristics are indeed a reflection of the Mediterranean climate, and the enclosed nature of the Mediterranean Sea. The irradiance over the Mediterranean area is about 20% greater than the mean irradiance incident at similar latitudes in the Atlantic Ocean (Bishop & Rossow, 1991). The Mediterranean Sea is also much saltier than average sea water, again as a result of the low precipitation and relatively high irradiance in the basin. The

distinctly oligotrophic nature of the Mediterranean Sea is, in turn, a consequence of the semi-enclosed nature of the basin which, along with the conditions above, leads to a net loss of nutrients across the Gibraltar Strait. Human activity in the Mediterranean basin has remained high for all the millennia since agriculture was first developed. Humans have altered the Mediterranean watersheds initially through forest clearances and more recently by intense agriculture and building dams. Thereby, the freshwater and inputs of associated materials to the sea have been drastically modified, acting as a major factor regulating the climate in the basin (cf. Rohling & Bryden, 1992; Martin & Milliman, 1997).

Efforts to examine the link between the marine climate of the Mediterranean and ecosystem structure and function have been either partial or locally restricted (e.g. Cacciamani, Nanni, Nucciotti & Paccagnella, 1992; Cebrián, Duarte & Pascual, 1996; Šolić, Krstulović, Marasović, Baranović, Pucher-Petković & Vucetić, 1997). As a consequence, the possible role of the Mediterranean marine climate as a template upon which ecosystems are structured remains untested. We provide here a synthesis of available information on the dynamic aspects of the Mediterranean climate and forcing it imposes on the ecosystem. We do so by focussing on both seasonal and decadal time scales. Because of the paucity of high resolution, coherent records of ecosystem dynamics in the Mediterranean Sea, this assessment is largely based on the examination of coastal ecosystems, predominantly in the Spanish coast, where records are available. Whenever possible we assess the generality of the patterns found for the Mediterranean Sea by comparing them to those observed elsewhere in the Mediterranean Sea, particularly in the Western Mediterranean.

The dynamics of the Mediterranean climate is described through the examination of sea surface temperature, atmospheric pressure, wave action, sea level, rainfall and the forcing exerted by humans. These properties are examined both at the short-term (subannual) and long-term (years to centuries) time scales. In addition to providing a description of the changes, through time-series plots, we also attempt to elucidate the dominant scales of variation, both at the seasonal and decadal time scales. Because of the poor quality of the data, with frequent gaps or heterogeneous sampling intervals, the time scales of variation are not examined through the classical Fourier analysis, whose assumptions are rather restrictive when compared to the characteristic of most of the data sets available for the Mediterranean Sea. Instead, we use a simpler, but more robust approach, the semivariogram (Isaaks & Srivastava, 1989). This technique examines how the difference between pairs of observations increases as their separation in time increases. The results allow the identification of the dominant time scales of variation (the sill in the semivariance vs. time scale plots), the occurrence of unstructured variation (white noise, the absence of coherent change in semivariance with increasing time scale), and cyclical variation (an undulating change in semivariance with increasing time scale).

2. Seasonal and decadal forcing in the Mediterranean climate

The Mediterranean climate is characterized by a clear seasonal forcing in irradiance, which, although subject to considerable interannual variability because

of variable cloud cover, leads to highly reproducible seasonal changes in surface temperature (Fig. 1). Mediterranean surface waters are relatively warm because the incident irradiance exceeds that received at similar latitudes of the Atlantic coasts of Europe by 20% (Bishop & Rossow, 1991). The seasonal thermocline develops around May–June, depending on the year, and a strong thermocline persists for 4–5 months until it is eroded by storms between mid-September and late October. Seasonality is the dominant source of short term (i.e. subannual) variability in surface water temperature, as reflected by the distinct peak in temperature semivariance at half a year, demonstrating its annual periodicity (Fig. 2).

Decadal variation in sea-surface water temperature is a relatively small source of variance in water temperature, characterized by a sequences of warm and cold years ($\pm 0.5^\circ\text{C}$ around the long-term mean) over the century (Fig. 3 and Table 1). Although there has been no clear monotonic trend in sea-surface temperatures during the 20th century (Fig. 3), a monotonic warming trend in deep waters is becoming increasingly clear (Bethoux, Gentili, Raunet & Tailliez, 1990; Rohling & Bryden, 1992; Bethoux & Gentili, 1996). This warming trend appears to be resulting from changes in circulation caused by reductions in freshwater inputs to the Mediterranean Sea (cf. Rohling & Bryden, 1992; Bethoux & Gentili, 1996; Roether et al., 1996; Martin & Milliman, 1997). Although weaker, there is also some evidence for a warming of surface sea water temperature over the past two decades (e.g. Marbà & Duarte, 1997), but evidence that this increase may be part of an oscillation, rather than represent a monotonic increase, is substantial (cf. Sashamanoglou & Makrogiannis, 1992). Examination of the variance structure of sea surface temperature at the decadal time scales reveals a dominant scale of variation at 13 years (Fig. 4), indicative of possible cycles with a periodicity of ca. 25 years (Table 1). This periodicity is consistent with previous observations that the dominant scale of variation in annual mean air temperature in the Mediterranean is 22 years, which corresponds to a similar variation in solar activity (Mazzarella & Palumbo, 1988).

The dynamics of Mediterranean surface water masses is greatly influenced by the atmosphere. Changes in atmospheric pressure directly influence sea level and wind, and hence wave height and turbulence (e.g. Cebrián et al., 1996). Atmospheric pressure in the western Mediterranean shows considerable variability at the seasonal scale with two main consistent seasonal features, (1) the onset of a high pressure system in late winter, from late January to March (Cacciamani et al., 1992; Marchetti, 1992; Cebrián et al., 1996) extending over two weeks to a month, depending on the year (Fig. 1), and (2) a high pressure system develops in the early fall (usually October), which persists for a shorter time than in the late winter system, but leads to a period of clear skies and stable weather known as St. Martin's summer (St. Martin's day is November 11) in NW Mediterranean countries (cf. Zingone, Cassotti, Ribera d'Alcala, Scardi & Marino, 1995). The characteristic time scale of annual changes in atmospheric pressure is about half a year, because of recurrent annual occurrence of the late winter high-pressure system (Fig. 2). The record also contains considerable 'white noise' variation at subseasonal (<150 days) time scales (Fig. 2).

These patterns of variation in atmospheric pressure probably have important consequences for the marine climate. Rapid changes in atmospheric pressure are associated

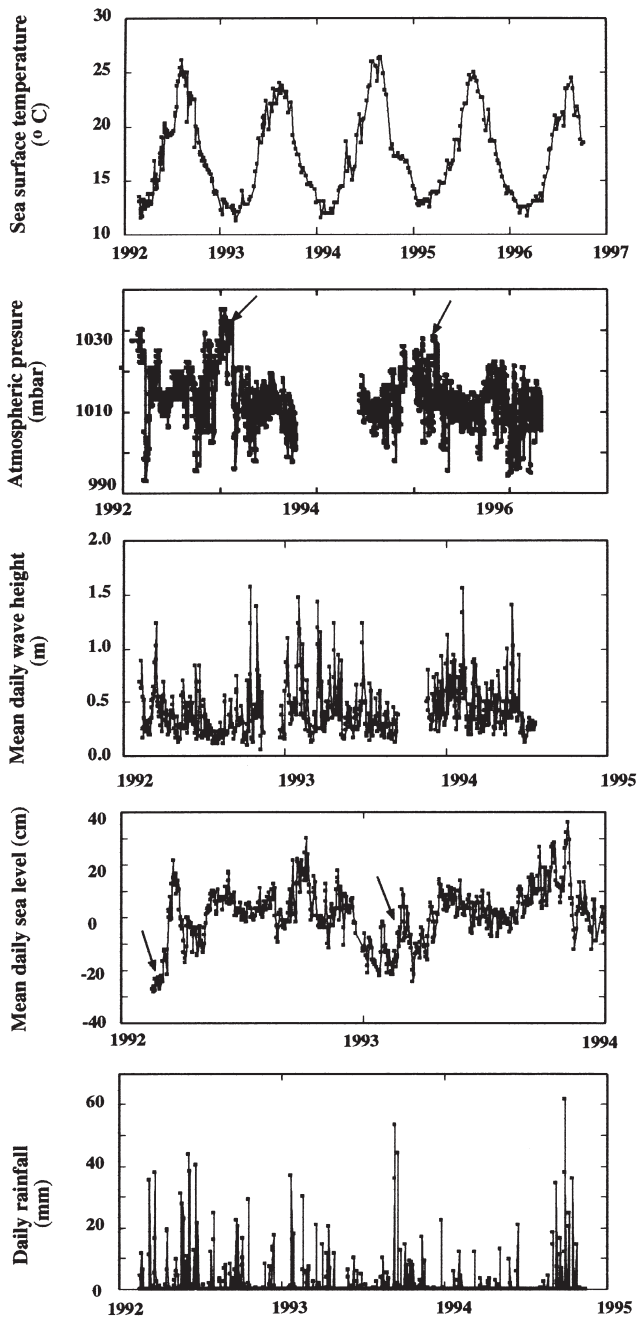


Fig. 1. Seasonal climatic patterns (mean daily sea surface temperature, mean daily atmospheric pressure, mean daily wave height, mean daily sea level and daily rainfall) in the NW Mediterranean (NE Spanish coast). From Duarte (unpubl. results). Arrows indicate features discussed in the text.

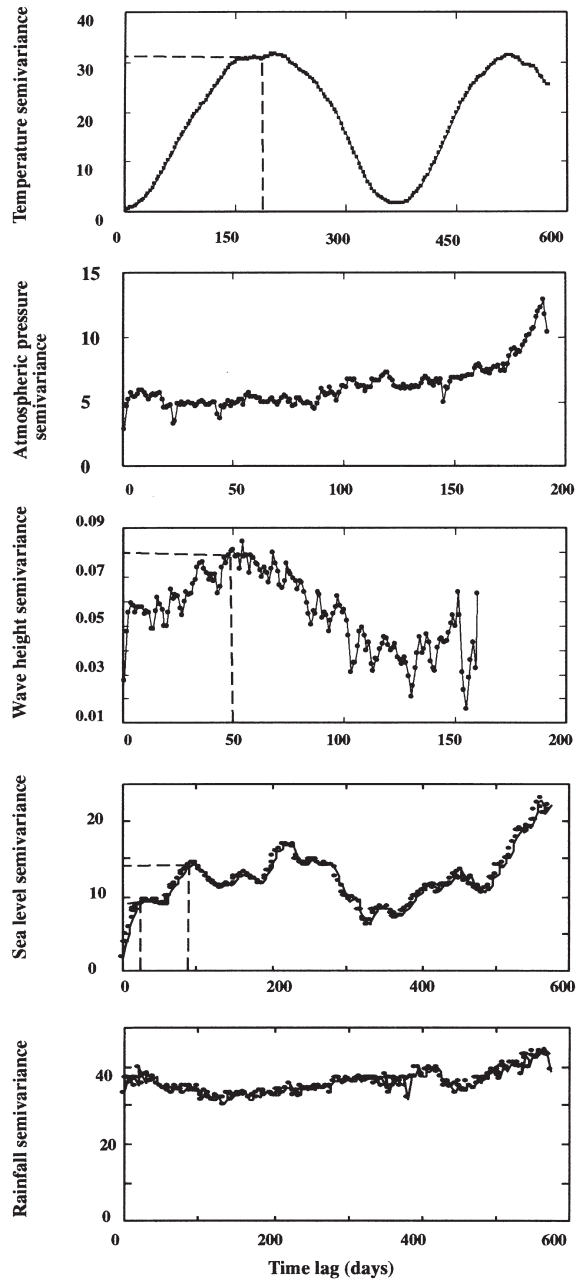


Fig. 2. Semivariograms showing the change in semivariance of the climatic properties in Fig. 1 with increasing time scale (i.e. time lag between pairs of observations). Dotted lines indicate the dominant scales of variation. Approximately flat curves are indicative of ‘white noise’ structure.

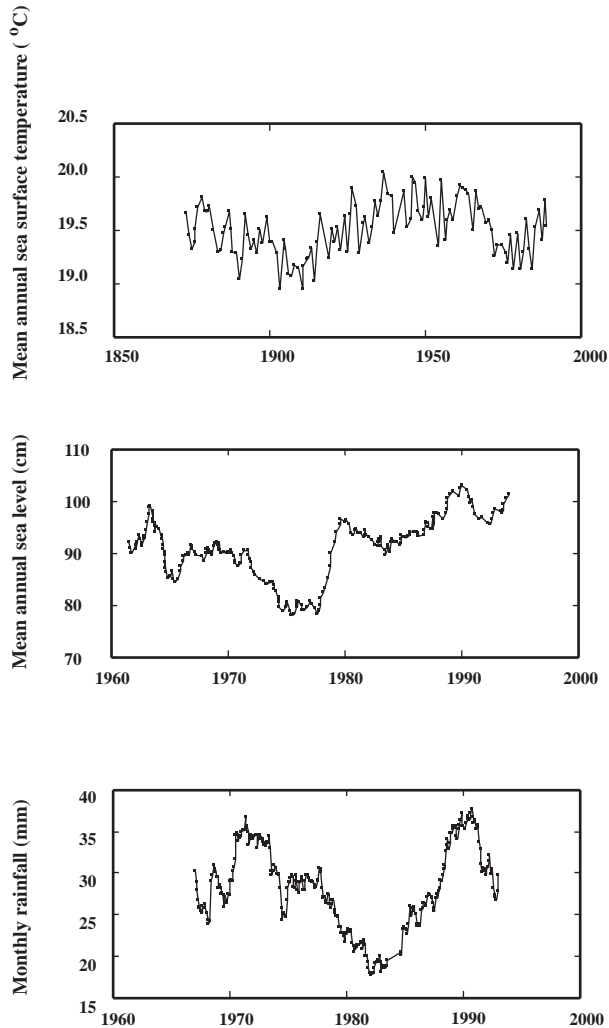


Fig. 3. Long-term variation in sea surface temperature across the Mediterranean (Metaxas, Bartzokas & Vitsas, 1991), and long-term changes in annual rainfall and sea level (data from Marbà & Duarte, 1997) in the NW Mediterranean (NE Spanish coast).

with the passage of frontal systems, which are associated with strong horizontal pressure gradients that are conducive to strong winds and large waves and high sea level in response to the low atmospheric pressure. In contrast, the extended periods of high atmospheric pressure are associated with weak horizontal pressure gradients with light winds and low wave heights (Marchetti, 1992). Wave height is, in general, moderate in the NW Mediterranean, but shows great variability at both seasonal and subseasonal time scales (Fig. 1). Despite a large short-term variability in wave height, the probability of high and low wave height shows a recurrent seasonal variation,

Table 1

Summary of dominant time scales of variation, trends and oscillations in key climatic factors in the Mediterranean Sea

Climate factor	Dominant time scale	Trend and oscillation	References
Sea surface temperature	Seasonal: 12 months	Min.: February, Max.: August	This study
	Long term: 3 and 11 years (ca. 22-year period)	Warm: 1940, 1965, 1990–date Cold: 1910, 1975–1980 Trend: +0.5°C/100 yr (surface) +0.36°C/100 yr (deep)	Mazzarella and Palumbo (1989) Metaxas et al., (1991) Bethoux and Gentili (1996) Marbà and Duarte (1997)
	Seasonal: 20–100 days	Min.: March, Max.: November	This study
Sea level	Long term: 5 and 11 years (ca. 22-year period)	Trend: +14.5 cm/100 yr.	Mazzarella and Palumbo (1988) Mazzarella and Palumbo (1989); Marbà and Duarte (1997)
	Seasonal: “white noise”	No clear seasonality	This study
Rainfall	Long term: 4 and 11 years (ca. 22-year period)	Moist: 1901–1921, 1930–1941 Dry: 1942–1954, 1980–1985	Maheras (1988) Marbà and Duarte (1997)

with the likelihood of low wave heights being during the periods of high atmospheric pressure in late winter and early fall, as well as mid summer (e.g. Marchetti, 1992; Cebrián et al., 1996). As a result, the variance structure of wave height shows a dominant time scale of 50 to 60 days (Fig. 2).

Sea level also shows variability along annual time scales. Seasonal events, such as an annual minimum in late winter (Fig. 1), coincide with the minimum in annual seawater temperatures and the highest atmospheric pressures. Sea level change in the Mediterranean is controlled by the interplay of atmospheric pressure (Tsimplis, 1995; Cebrián et al., 1996) and seasonal thermal expansion (Cebrián et al., 1996). Hence, the seasonal variance of sea level combines the variances of surface seawater temperature and atmospheric pressure resulting in a complex pattern of variance time scales. The dominant time scales are at about three weeks and three months (Fig. 2) and an increase in semivariance at time scales longer than annual, indicates the presence of longer-term trends in sea level. Indeed, examination of long-term changes in sea level provides evidence of sea level rise in the NW Mediterranean (Fig. 3), although it may be part of a long-term oscillatory behaviour rather than a sustained rising sea level. The variance structure of sea level at decadal time scales shows a dominant scale of variation at about 12–13 years, coherent with solar sunspot vari-

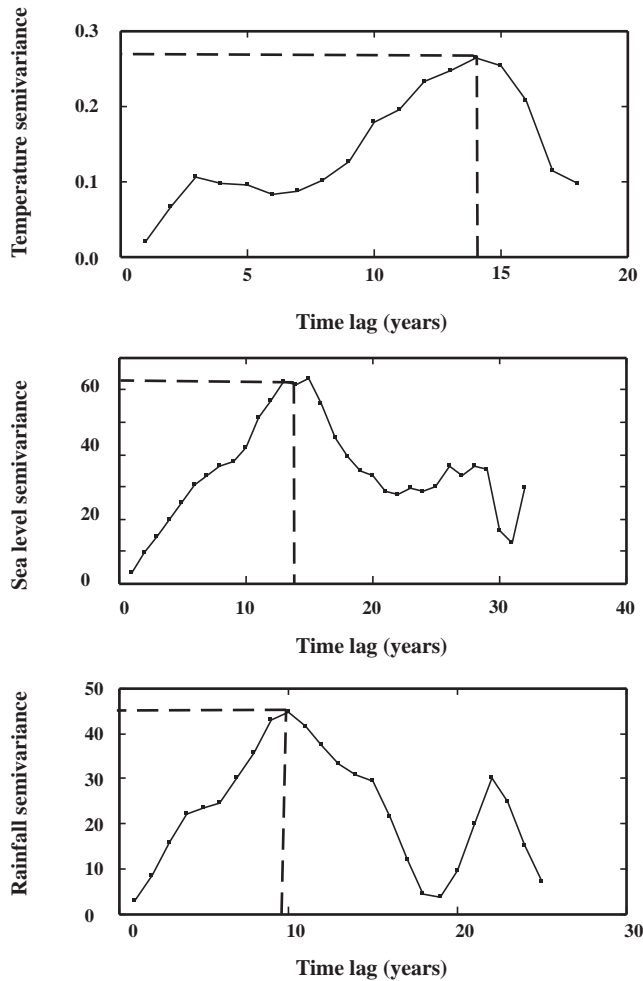


Fig. 4. Semivariograms showing the change in semivariance of the long-term changes in climatic properties in the NW Mediterranean (NE Spanish coast) with increasing time scale (i.e. time lag between pairs of observations). Dotted lines indicate the dominant scales of variation.

ation (Mazzarella & Palumbo 1988, 1989), and reflected in the variance of decadal changes in sea water temperature (Table 1). These oscillations are of a much greater amplitude than the upward trend in rising sea level (14 cm since 1890, and 50 cm over the past 2000 years, Table 1), which is largely accounted for by expansion resulting from long-term warming (Mazzarella & Palumbo 1988, 1989; Marbà & Duarte, 1997).

Freshwater input has an overriding effect on the dynamics of the Mediterranean ecosystem, it affects mesoscale circulation, deep-water formation, exchanges with the Atlantic, and the input of materials from land (Rohling & Bryden, 1992;

Bethoux & Gentili, 1996; Roether et al., 1996; Martin & Milliman, 1997). Rainfall, however, shows extreme variability at the seasonal time scale (Fig. 1) (e.g. Lautensach, 1967). There is as much variance in rainfall between consecutive days as there is between seasons, so rainfall patterns behave as a random factor at seasonal time scales. This results in a ‘white noise’ pattern when the seasonal time scales of variation are examined (Fig. 2). In contrast, examination of decadal patterns in rainfall reveals that there are oscillations between wet and dry periods (Fig. 3), which are coherent across the Western Mediterranean (Maheras, 1988). Decadal changes in rainfall involve, in particular, a dominant time scale of variation of about 10 years, indicative of a oscillation with ca. 20-year periodicity which is again close to those already described for sea level and sea water temperature (Fig. 4 and Table 1). Changes in annual rainfall in the Mediterranean basin are affected by the occurrence of extreme storms which contribute a significant percentage of the annual rainfall. The oscillations described involve changes in the occurrence and strength of these storms between moist and dry periods (Lautensach, 1967). These storms have a major impact on the coastal environment. They are associated with abrupt drops in atmospheric pressure, sea level rise and enhanced wave action, which cause high rates of erosion and inflict great damage to coastal structures (Sestini, 1989).

This discussion of the Mediterranean climate indicates that it is only sea surface temperature which follows a simple unimodal pattern of seasonal variation. Atmospheric pressure and the associated changes in sea level and wave action show some seasonality (e.g. high atmospheric pressure, calm waters and low sea level in late winter), but their greatest variance is at short time scales (50–100 days; Fig. 2 and Table 1). Rainfall behaves as a white noise at the seasonal time scale, which adds complexity to attempts to predict the Mediterranean marine climate and its associated ecosystem dynamics. The differences in the variance structure of climate factors at the seasonal and subseasonal time scales contrast with the coherence observed in changes occurring at decadal time scales. The dominant period of change is 22 years (Table 1), which reflects solar forcing. The evidence for long-term sustained trends of increasing sea surface temperature and sea level is masked by these decadal oscillations, which render their detection difficult, although increasingly apparent (Table 1).

3. Anthropogenic forcing as a major factor in marine climate

The evidence for the existence of sustained long-term trends of warming in the waters and increased sea level points to an anthropogenic forcing of the Mediterranean climate. Indeed, humans have directly affected the climate of the Mediterranean basin for centuries, particularly by influencing the discharge of freshwater. Many Mediterranean rivers, mostly those in the southern half of the basin are intermittent, being dry for most of the year and flushed abruptly following storms. Discharge during these flood events shows a 100-fold increase over the mean annual discharge, and at times cause great damage (Lautensach, 1967). The frequency of these sudden river flushes (spates) has been altered as a result of human manipulation

of the watersheds, deforestation and associated processes have increased water runoff. These influences are clearly seen in the intermittent increases in the frequency of spates in the Segura River, the major river in SE Spain, over the past millennium (Fig. 5). These maxima correspond to specific political situations which have resulted in widespread deforestation in Spain: the massive construction of ships associated to the forging of the Spanish colonial empire (XV–XVI centuries); and the two periods (XVIII and XIX century) when the land held personally by the catholic church ('unproductive hands') was given to farmers ('productive hands').

Human pressure in the Mediterranean basin is a major factor in climate change both at the decadal and seasonal time scales. Population growth rate in the Mediterranean basin is exponential (Fig. 6). The number of tourists has doubled every 15 years since the 1960's and the permanent population is forecast to double in the next 30 years (Fig. 6). Such increases in population have major consequences, largely related to the associated demands for freshwater resources. Water discharged into the sea from NW Mediterranean coastal towns is now strongly seasonal (Fig. 7), as a consequence of the summer influx of tourists, which typically generates a 2- to 10-fold increase in the populations of the coastal towns. There is also a strongly seasonal discharge of nutrients to the sea (Fig. 7) peaking when the summer thermocline would otherwise lead naturally to the development of nutrient poor waters. In addition, overexploitation of the aquifers to meet the demands for water for both the growing resident and tourist populations is leading to widespread subsidence along the NW Mediterranean coastline, enhancing the rate of sea level rise (by up to 5-fold, cf. Milliman, 1992). Increasing sea level rise leads, in turn, to increased sediment erosion, which creates demands for extensive investments in coastal protection and beach replenishment programmes. The widespread construction of dams on Mediterranean rivers has led to considerable reductions in sediment delivery (up to 90% reduction in some rivers, Martin & Milliman, 1997) to the sea, further exacerbating the problems of coastal erosion (e.g. Sestini, 1989).

These observations make it clear that human pressure is so strong in the Mediterranean basin that anthropogenic influences have become key climatic factors, influ-

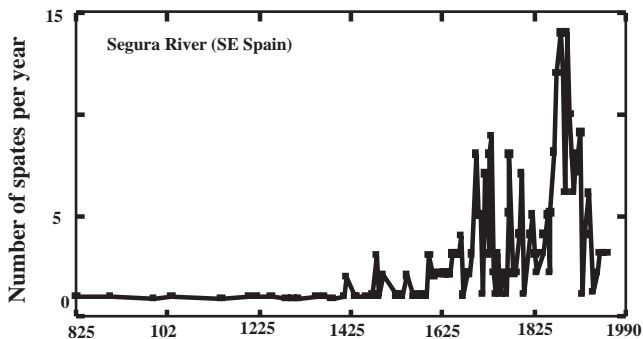


Fig. 5. The time course of the number of spates (abrupt flushing of otherwise semidry rivers) in the Segura River (SE Spain). Data from Lopez Bermudez, Calvo and Morales (1986).

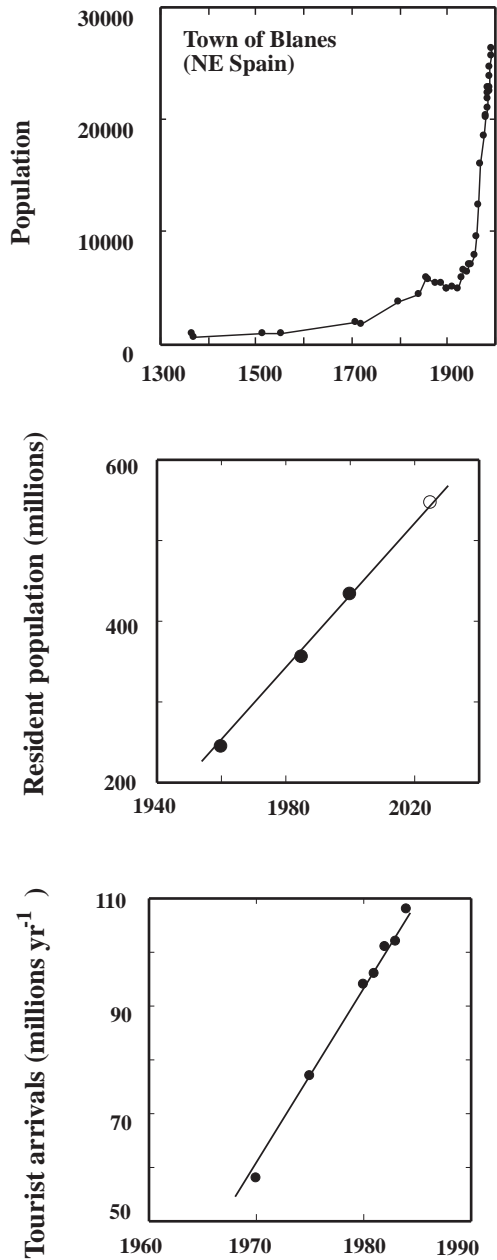


Fig. 6. Evolution of human population in the town of Blanes (NE Spain), and trends in population (resident and visitors) in the Mediterranean basin (data from UNEP, 1989). The open circle indicates a projected estimate.

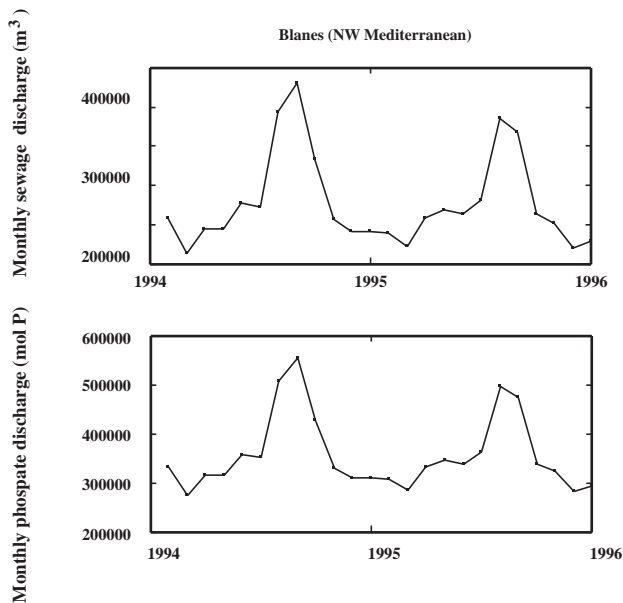


Fig. 7. The seasonal pattern of sewage, and associate phosphate, discharge to the Mediterranean Sea from the town of Blanes (resident population 20,000, seasonal maximum about 130,000), a tourist-oriented town in NE Spain. Data from Duarte (unpubl. results).

encing water and nutrient discharge to the Mediterranean, as well as contributing to sea level rise and coastal erosion. Contrary to the patterns observed in other components of marine climate, human forcing has a distinct seasonal pattern. However, human pressure shows a steady, possibly accelerating, upward long term trend, contrasting with the dominant 22 years oscillation displayed by other components of the marine climate (Fig. 4, Table 1).

4. Seasonal and decadal forcing in the Mediterranean ecosystem

Temperature is a key controlling factor for many biological rate processes. The clear seasonal pattern of sea surface temperature, with a 14°C amplitude in the NW Mediterranean (12–26°C), suggests that biological processes should also show a clear seasonality. This is shown, for instance, in the patterns of zooplankton abundance (Mazzocchi & Ribera D'Alcala, 1995; Andreu & Duarte, 1996) and in plankton community respiration (e.g. Satta, Agustí, Mura & Duarte, 1996). The growth, biomass and production of benthic macrophytes also tend to be higher in summer (e.g. Alcoverro, Duarte & Romero, 1995), although this seasonal pattern is less clear in fast (e.g. Marbà, Cebrián, Enríquez & Duarte, 1996a) and slow-growing (Vidondo & Duarte, 1995) macrophytes.

The abundance and production of phytoplankton, however, shows no clear evi-

dence of a unimodal seasonality (Fig. 8). The reason for this may be the higher irradiance (20% higher) and water temperature (3–5°C higher) in the Mediterranean compared to similar latitudes in the Atlantic, which results in the Mediterranean winter climate sustaining better phytoplankton growth; the development of a late-winter (February to March) phytoplankton bloom (Fig. 8) is one of the most coherent seasonal features of Mediterranean phytoplankton communities (cf. Scotto Di Carlo, Tomas, Ianora, Marino, Mazzocchi, Modigh et al., 1985; Cacciamani et al., 1992; Modigh, Saggiomo & Ribera d'Alcala, 1996; Mura et al., 1996a). The late winter phytoplankton bloom develops during a period of high atmospheric pressure and stable water column (Marchetti, 1992; Cacciamani et al., 1992; Cebrián et al., 1996). The clear skies and stable water column at this time lead to a relatively high irradiance, able to support light-saturated photosynthetic rates (Satta et al., 1996), which, together with the relatively high nutrient concentrations following winter mixing, lead to fast phytoplankton growth (Mura et al., 1996a; Mura, 1997). Similar conditions are reproduced, albeit for a shorter (<2 weeks) time span, during the period of high atmospheric pressure and associated high irradiance and stable waters

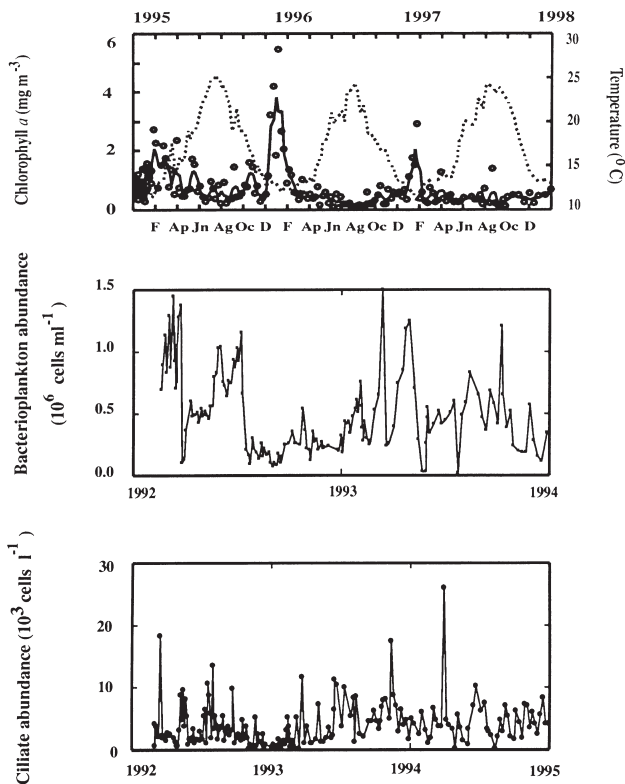


Fig. 8. The seasonal pattern of change in planktonic chlorophyll *a* concentration and temperature, bacterial abundance, and ciliate abundance in Blanes Bay surface waters (NE Spain). Data from Vaqué et al. (1997), and Agustí (Unpubl. results).

in the fall ('St. Martin's summer'). At this time nutrient concentrations are relatively high, as a result of the erosion of the seasonal thermocline and the increases in freshwater discharge associated to the late-summer storms. These conditions also lead to a recurrent algal bloom in early fall (cf. Zingone et al., 1995; Mura et al., 1996b).

The late winter phytoplankton bloom is the main clue for seasonal ecosystem processes. It occurs at a time when zooplankton populations are low (Mazzocchi & Ribera D'Alcala, 1995; Andreu & Duarte, 1996), probably because of the lack of suitable food in winter and high predation rates by sardine larvae spawned just before the bloom (cf. Palomera & Olivar, 1996). The low herbivore pressure in surface waters results in a high carbon flux to the benthos and the mass release and subsequent recruitment to the benthos of larvae of benthic invertebrates. However, a closer examination of the relationship between benthic reproduction and the late winter phytoplankton bloom clearly shows that this is not a simple cause-effect relationship. The allocation of resources to gonad growth and maturation often starts well before the onset of the late winter bloom (e.g. a couple of months in sea urchins). Hence, the bloom does not trigger benthic reproduction directly, but it influences its success (López, Turón, Montero, Palacín, Duarte & Tarjuelo, 1998). The occurrence of the late winter period of calm waters and of relatively high irradiance which leads to the development of the bloom appears to be such a recurrent feature that it is imprinted in the life history of the ecosystem components. This is the case for sardines which spawn at the start of this period (cf. Palomera & Olivar, 1996), and the majority of benthic invertebrates that reproduce at this time (e.g. López et al., 1998), thereby maximizing the likelihood of survival of their larvae. Despite the importance of this event for the ecosystem, the late winter Mediterranean bloom is yet to be recognized as a major component of the seasonality of the system or to be incorporated into models.

The seasonal pattern of Mediterranean phytoplankton growth leads to a complex variance structure (Fig. 9), involving a characteristic time scale of change of about 50 days (Prairie & Duarte, 1996). This pattern is shared by the abundance of other components of the planktonic ecosystem, such as bacteria and ciliates (Fig. 8), giving a time scale of variation at about 60 days (Fig. 9). The time scales of seasonal change of microplanktonic communities are coherent with those of sea level and wave action (Fig. 2), whose variations, therefore, appear to drive the variability of the planktonic system. Clearly, the link between planktonic variation and that in sea level and wave action does not result from a direct cause-effect relationship, but rather through the influence of the ultimate effect of these climatic factors on the proximal factors, such as nutrient inputs and water column stability, influencing planktonic organisms. The seasonal variance structure of the abundance of planktonic components also contains considerable noise (Fig. 9), suggesting the importance of random, temporally-unstructured processes. These may result partially from interactive processes leading to complex behaviour, but may also reflect the importance of rainfall and the occurrence of storms as factors influencing the ecosystem. Storms are associated with high discharge of suspended material, which leads to a deterioration in conditions for phytoplankton growth. This exerts a considerable influence on heterotrophic

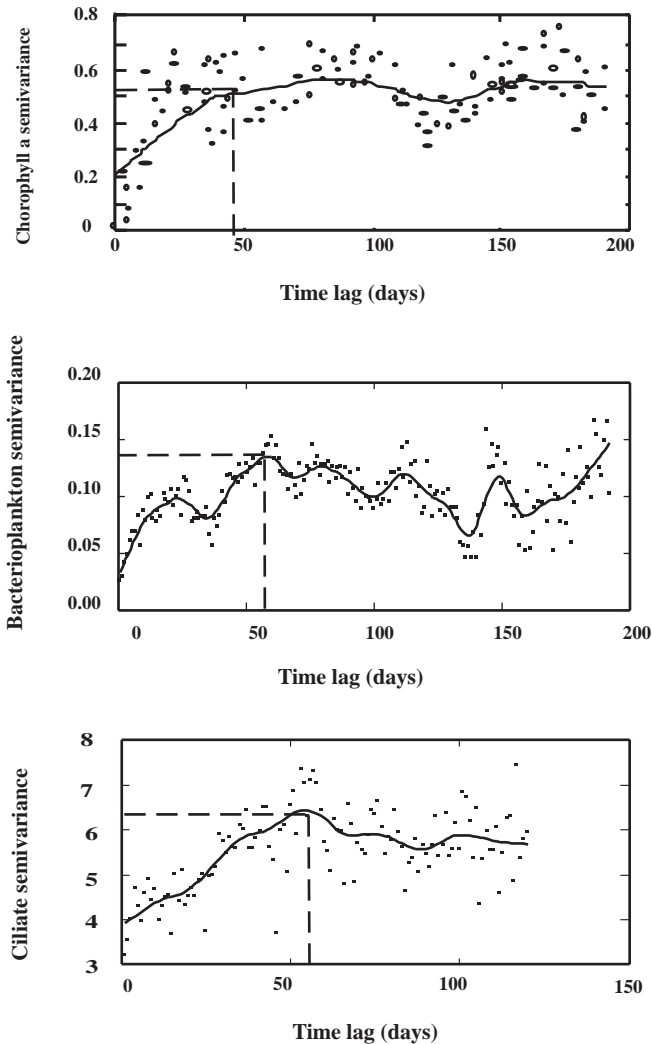


Fig. 9. Semivariograms showing the change in semivariance of the seasonal changes in planktonic chlorophyll a concentration, bacterial abundance, and ciliate abundance in Blanes Bay (NE Spain) with increasing time scale (i.e. time lag between pairs of observations). Dotted lines indicate the dominant scales of variation. Solid lines are an smooth representation of the data.

microplankton as well (e.g. Vaqué, Blough & Duarte, 1997). As a result, the seasonal temporal pattern of microplanktonic organisms is highly variable, in contrast with the more recurrent patterns observed in other temperate waters.

While seasonal forcing involves substantial variation, derived from the largely unstructured nature of many of the forcing climatic factors, these factors show

remarkably clear and coherent patterns of variation at the decadal time scale, involving a 22 years periodicity. It is, therefore, expected that this periodicity be somehow reflected in the long-term changes of ecosystem components and processes. Unfortunately, at present there is a severe paucity of long-term records in the Mediterranean (Duarte, Cebrián & Marbà, 1992), which prevents a direct testing of whether these changes in climate are paralleled by changes in ecosystem structure and function. There is, however, evidence that changes are indeed taking place (Table 2), but most of this evidence is based on either anecdotal or scattered information, which is unable to clearly identify whether or not the changes represent monotonic trends as evidence of human effects, or are part of long term oscillations coherent with the 22-year oscillation of climatic factors in the Mediterranean. Indeed, available long-term records of changes in some ecosystem components do provide evidence of a dominant oscillatory behaviour (e.g. Mazzocchi & Ribera D'Alcala, 1995; Marbà & Duarte, 1997; Šolić et al., 1997).

Table 2
Summary of reported ecosystem change in the Mediterranean Sea

Property	Trend	Region	References
Water transparency	Decline	NW Mediterranean	Marbà and Duarte (1997)
Nutrient concentrations	Increase	Adriatic Sea	Justić (1988)
		NW Mediterranean	Bethoux et al. (1990) Rohling and Bryden (1992) Bethoux and Gentili (1996)
Primary production	Increase	Adriatic Sea	Justić (1988)
Phytoplankton biomass	Increase	Adriatic Sea	Šolić et al. (1997)
Bacteria abundance	Increase	Adriatic Sea	Šolić et al. (1997)
Seagrass abundance	Decline	NW Mediterranean	Marbà & Duarte (1997)
Seagrass vertical growth	Decline	NW Mediterranean	Marbà & Duarte (1997)
Fish landings	Increase	Mediterranean Sea	Caddy, Refk and Do-Chi (1995)
Fish trophic level	Decline	Mediterranean Sea	Pauly, Christensen, Dalsgaard, Froese and Torres (1998)
Species composition	Increase of termophilic species (fish, algae, echinoderms)	NW Mediterranean	Francour, Bouderesque, Harmelin, Harmelin-Vivien, and Quignard (1994)
		Ligurian Sea	Astraldi, Bianchi, Gasparini and Morri (1995)

The long-term record of water transparency (Secchi disc depth) presented in Fig. 10, which correlates with phytoplankton biomass, shows a declining trend of $-0.10 \pm 0.01 \text{ m yr}^{-1}$ in the NW Mediterranean (Marbà & Duarte, 1997). This trend dominates the long-term variance structure of the water transparency, resulting in an upward, linear trend in the semivariogram (Fig. 10). Such variance structure is consistent with human pressure, but it is the only component of climate showing a clear monotonic rather than oscillatory trend. This trend of reducing water transparency provides further evidence for the deterioration of water quality in the Mediterranean littoral (Marbà & Duarte, 1997). In conjunction with the increased nitrogen and phosphorus concentrations (Bethoux & Gentili, 1996) observed elsewhere, it suggests that eutrophication is likely to become a widespread problem in Mediterranean coastal waters.

The finding of decreasing water transparency in the NW Mediterranean has important consequences for the ecosystem, such as the loss of seagrasses and other benthic plants (e.g. Sand-Jensen & Borum, 1991; Duarte, 1995). The transparency

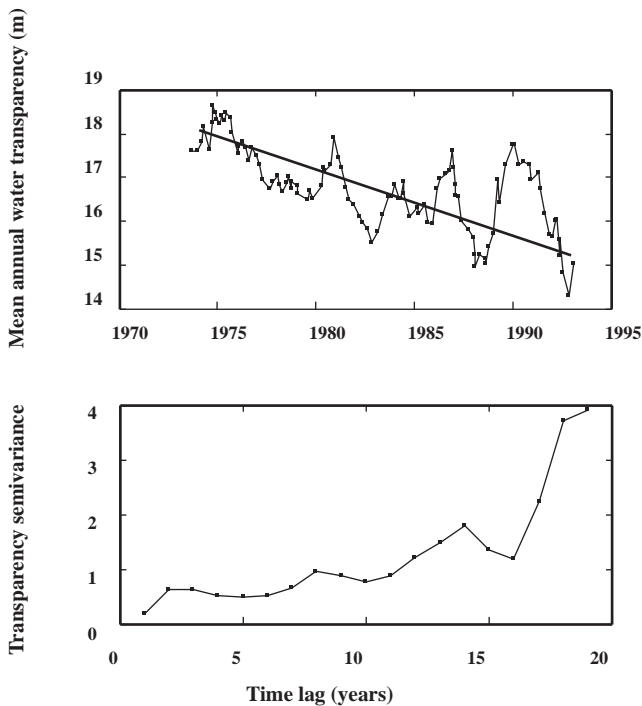


Fig. 10. Long-term changes in water transparency (as the depth of visibility of the Secchi disc) in NE Spain coastal waters (data from Marbà & Duarte, 1997), and the semivariograms showing the increase in variance with increasing time lag.

of the water controls the maximum depth to which seagrass meadows can develop. The equation (recalculated from Duarte, 1991):

$$\text{Depth limit (m)} = 1.1 \text{ Secchi depth (m)}$$

predicts that the depth limit of *Posidonia oceanica*, the dominant seagrass species in the Mediterranean, will have been reduced by 4 m during the observational period, and this is consistent with observations in the area where the water transparency has been recorded. It is clear, therefore, that the regression of *Posidonia oceanica* meadows in the NW Mediterranean is, in part, linked to eutrophication processes. However, the decline of seagrasses has also been observed in shallow areas, and so cannot be directly accounted for by the reduced transparency of the waters (Marbà, Duarte, Cebrián, Enríquez, Gallegos, Olesen et al., 1996b). A survey of 29 *Posidonia oceanica* shallow (3–10 m) meadows along the Spanish Mediterranean coast showed 57% of the meadows are in decline, sufficient to involve — if maintained at the rates observed — a loss of 50% of the seagrass cover in 2 to 24 years (Marbà et al., 1996b). While locally there were some perturbations in nutrient inputs which may account for the observed decline, this was not the case for all of the meadows, and for many there were no obvious point sources for anthropogenic disturbance. Hence, local perturbations may account for the widespread decline of *Posidonia oceanica* in the NW Mediterranean only in part and large-scale, climatic factors must also be involved. The elucidation of such climatic influences is currently precluded by the absence of time series which would provide the capacity to test them. We have shown that there is a link between climate variation and ecosystem functioning at the seasonal scale which, in itself, suggests that the substantial changes in climate over the past decades must also have had major impact on the Mediterranean ecosystem.

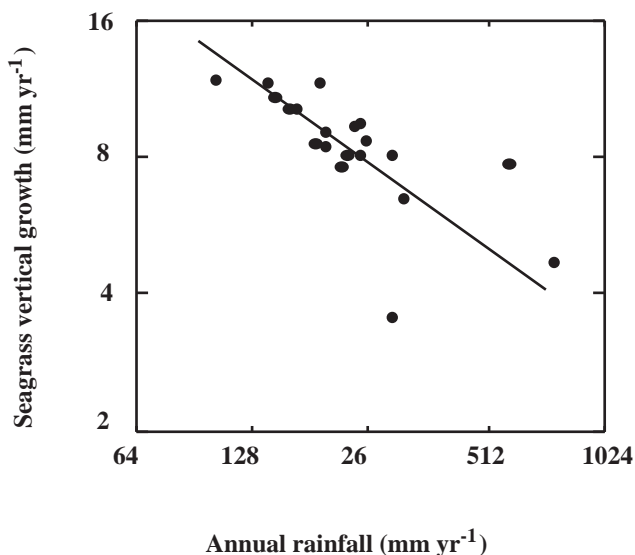
5. Long-lived organisms as witnesses of long-term change in Mediterranean ecosystems

The paucity of long-term records of change in the Mediterranean ecosystem should foster efforts to ensure that in future the necessary data are collected. Yet, the changes that are taking place are so important and their consequences for the environment and society so severe, that the option to wait for adequate data sets to be compiled over the coming decades is simply unacceptable. It is, therefore, urgent for the ecosystem itself to be probed for clues as to the nature of the changes that are taking place. Traditional paleoceanographic techniques cannot, however, fully satisfy this demand, for they provide records of change over time scales (millennia) which are much longer than those relevant to society (decades).

An alternative option, which we strongly advocate, is the use of long-lived organisms as witnesses of change. The oligotrophic nature of the Mediterranean Sea has led to the proliferation of long-lived organisms within its benthic communities. For instance, the dominant seagrass, *Posidonia oceanica*, in the Mediterranean Sea is the longest lived autotroph in the ocean. *Posidonia oceanica* shoots live for up to

half a century (Marbà et al., 1996b) and the clones have been dated to be over 4,000 years old (Mateo, Romero, Pérez, Littler & Littler, 1997). The balloon-like macroalga *Codium bursa*, which forms lush communities in the Mediterranean, must also rank amongst the slowest growing autotrophs in the world ocean (Vidondo & Duarte, 1995). It is able to reach large sizes (>40 cm in diameter, Geertz-Hansen, Enriquez, Duarte, Agustí, Vaqué & Vidondo, 1994), indicating that this unique macroalga has a particularly long life span (Vidondo & Duarte, 1998). The Mediterranean Sea also harbours *Pinna nobilis*, the largest bivalve in the temperate zone, whose shell attains lengths of 80 cm and whose life span is several decades (Butler, Vicente & De Gaulejac, 1993). No doubt specimens of these organisms and other long-lived species in the Mediterranean Sea, have records of these climatic changes within their structures. These organisms could provide an insight into the ecosystem responses to changes if they could be appropriately interrogated. Adequate techniques to reconstruct these responses are available, involving, for example, the use of growth marks in seagrass shoots (Pergent & Pergent-Martini, 1990; Duarte et al., 1994), and changes in the stable isotope composition of the calcite of molluscs (e.g. Arthur, Williams & Jones, 1983).

The reconstruction of the vertical growth of the reef-forming rhizomes of *Posidonia oceanica* along the Spanish Mediterranean coast provides insight into local changes in the sedimentary balance, for seagrass vertical growth has been demonstrated to be coupled to the balance between sediment inputs and loss at time scales both short (Marbà & Duarte, 1994) and long (Mateo et al., 1997). Changes in the rate of vertical growth of *Posidonia oceanica* shoots in shallow water depths (3–10 m) have been characterized by a declining trend in the past decade, as well as by an oscillatory behavior, suggesting alternating episodes of sediment erosion and accretion (Marbà & Duarte, 1997). This trend of declining vertical growth of *Posidonia oceanica* shoots indicates a reduction in sedimentation rates and a widespread erosion in these shallow seagrass meadows, consistent with the severe beach erosion problems experienced along the Spanish Mediterranean coast. Oscillations in vertical growth, in general, show characteristic time scales at about 7 and 25 years, matching the variance structure of decadal variation in rainfall at the sites where the seagrasses have been investigated (Marbà & Duarte, 1997). Indeed, changes in annual rainfall have been found to be significantly negatively correlated with changes in the average vertical growth of *Posidonia oceanica* shoots (Fig. 11), suggesting that erosion of the beds increases during wet years (cf. Meade & Emery, 1971). Leaf production rates also showed an oscillatory behaviour (Marbà & Duarte, 1997), but there was no real evidence of a consistent trend along the Spanish Mediterranean coast. These results show that, while water quality, which determines seagrass performance, may have deteriorated where anthropogenic disturbance is high, this effect cannot explain the widespread tendency towards seagrass decline (Marbà et al., 1996b). The decline thus appears attributable, instead, to increased coastal erosion. Moreover, the loss of seagrasses, which effectively protect sediments, can be expected to lead to further acceleration in coastal erosion. Thus reconstruction of the production and vertical growth of *Posidonia oceanica* shoots enable its response to climate change in the NW Mediterranean to be assessed, and discrimination made between local and gen-



1993; Richardson et al., 1999) make it possible to collect samples of shell material that allows the resolution of isotopic changes in calcite at weekly time scales (Richardson et al., 1999).

The examination of in situ temperature inferred from *Pinna nobilis* collected from SE Spain (Fig. 12) provides the resolution of seasonal events which are in excellent agreement with measured in situ temperature. The records of $\delta^{13}\text{C}$ in the calcite also display a distinct seasonality (Fig. 12). These measurements, when corrected for possible metabolic effects (cf. Tanaka, Monaghan & Rye, 1986; Klein, Lohmann & Thayer, 1996; Mcconnaughey et al., 1997), have the potential to provide records of changes in the isotopic composition of dissolved inorganic carbon in Mediterranean surface waters from which can be drawn inferences on the seasonal and decadal fluctuations in community metabolism, as well as progression rate of invasion of anthropogenic CO_2 into the Mediterranean Sea. *Pinna nobilis* is widespread in the Mediterranean, so sets of records from a number of locations can be acquired to examine the coherence of the changes at the basin scale.

These examples clearly demonstrate how studies of long-lived organisms have the potential to discriminate decadal-scale changes in the Mediterranean ecosystem, and hence bridge the gap resulting from the paucity of direct records. Unfortunately,

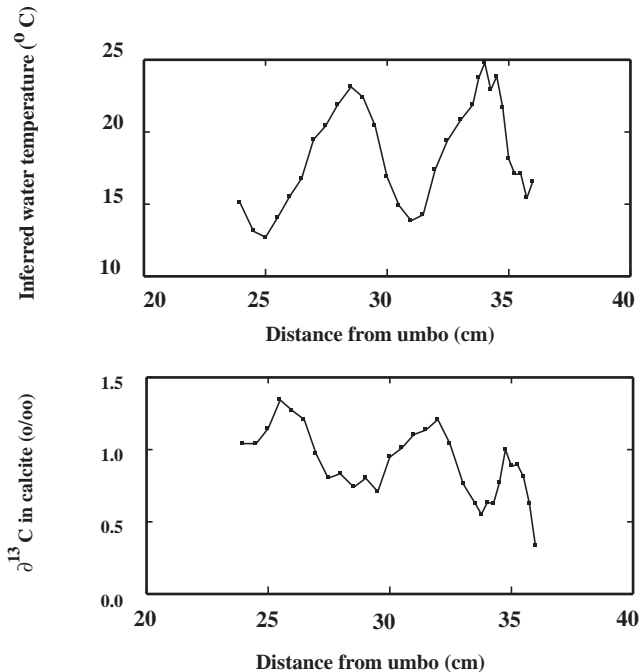


Fig. 12. Changes in inferred temperature (from ^{18}O) and the $\delta^{13}\text{C}$ signature of the calcite of the large bivalve *Pinna nobilis* collected in the coast of semi-arid SE Spain (Aguamarga) with distance from the umbo (data from Kennedy, unpubl. results). This distance provides a proxy for time, allowing the elucidation of seasonal patterns in these signals.

long-lived organisms that have the potential to provide important services, such as their use as recorders of change are particularly sensitive to perturbations. Populations of both *Posidonia oceanica* and *Pinna nobilis* are in steep decline in the Mediterranean.

The importance of the changes reported here, both in terms of the potential ecological and socioeconomic impacts, requires their nature to be investigated as a matter of urgency. A coherent system of observation needs to be established so that local to mesoscale to basin-scale effects can be elucidated, and trends, which may only represent a small percent of the variance, can be discriminated from oscillatory behaviour. Such an observational system is likely to yield basic information that will be relevant beyond the scope of the Mediterranean basin, whose reactivity to climate may be used as a ‘miner’s canary’ for global change.

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References

- Alcoverro, T., Duarte, C. M., & Romero, J. (1995). Annual growth dynamics of *Posidonia oceanica*: Contribution of large-scale versus local factors to seasonality. *Marine Ecology Progress Series*, 120, 203–210.
- Andreu, P., & Duarte, C. M. (1996). Seasonality of zooplankton in the Bay of Blanes. In C. M. Duarte, *Seasonality in the Blanes Bay: a paradigm of the northwest Mediterranean littoral. Publicación Especial*, (pp. 47–54) vol. 22. Instituto Español de Oceanografía.
- Arthur, M. A., Williams, D. F., & Jones, D. S. (1983). Seasonal temperature-salinity changes and thermocline development in the Mid-Atlantic Bight as recorded by the isotopic composition of bivalves. *Geology*, 11, 655–659.
- Astraldi, M., Bianchi, C. N., Gasparini, G. P., & Morri, C. (1995). Climatic fluctuations, current variability and marine species distribution: a case study in the Ligurian Sea (north-west Mediterranean). *Oceanologica Acta*, 18, 139–149.
- Bethoux, J. P., & Gentili, B. (1996). The Mediterranean Sea, coastal and deep-sea signatures of climatic and environmental changes. *Journal of Marine Systems*, 7, 383–394.
- Bethoux, J. P., Gentili, B., Raunet, J., & Tailliez, D. (1990). Warming trend in the western Mediterranean deep water. *Nature, London*, 347, 660–662.
- Bishop, J. K. B., & Rossow, W. B. (1991). Spatial and temporal variability of global surface solar irradiance. *Journal of Geophysical Research*, 96, 16839–16858.
- Butler, A. J., Vicente, N., & De Gaulejac, B. (1993). Ecology of the pteroid bivalves *Pinna bicolor* Gmelin and *Pinna nobilis* L. *Marine Life*, 3, 37–45.
- Cacciamani, C., Nanni, S., Nuccioti, F., & Paccagnella, T. (1992). Analysis of meteorological parameters

- relating to Adriatic eutrophication. In R. A. Vollenweider, R. Marchetti, & R. Viviani, *Marine coastal eutrophication. Science of the Total Environment Suppl* (pp. 159–170).
- Caddy, J. F., Refk, R., & Do-Chi, T. (1995). Productivity estimates for the Mediterranean: evidence of accelerating ecological change. *Ocean and Coastal Management*, 26, 1–18.
- Cebrián, J., Duarte, C. M., & Pascual, J. (1996). Marine climate in the NW Mediterranean littoral. In C. M. Duarte, *Seasonality in the Blanes Bay: a paradigm of the northwest Mediterranean littoral. Publicación Especial*, (pp. 9–21) vol. 22. Instuto Español de Oceanografía.
- Duarte, C. M. (1991). Seagrass depth limits. *Aquatic Botany*, 40, 363–377.
- Duarte, C. M. (1995). Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, 41, 87–112.
- Duarte, C. M., Cebrián, J., & Marbà, N. (1992). Uncertainty of detecting sea change. *Nature London*, 356, 190.
- Duarte, C. M., Marbà, N., Agawin, N., Cebrián, J., Enríquez, S., Fortes, M. D., Gallegos, M. E., Merino, M., Olesen, B., Sand-Jensen, K., Uri, J., & Vermaat, J. (1994). Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Marine Ecology Progress Series*, 107, 195–209.
- Francour, P., Bouderesque, C. F., Harmelin, J. G., Harmelin-Vivien, M. L., & Quignard, J. P. (1994). Are the Mediterranean waters becoming warmer? Information from biological indicators. *Marine Pollution Bulletin*, 28, 523–526.
- Geertz-Hansen, O., Enriquez, S., Duarte, C. M., Agustí, S., Vaqué, D., & Vidondo, B. (1994). Functional implications of the form of *Codium bursa*, a balloon-like Mediterranean macroalga. *Marine Ecology Progress Series*, 108, 153–160.
- Isaaks, E. H., & Srivastava, R. M. (1989). *Applied geostatistics*. Oxford: Oxford University Press.
- Justić, D. (1988). Trend in the transparency of the Northern Adriatic Sea 1911–1982. *Marine Pollution Bulletin*, 19, 32–35.
- Klein, R. T., Lohmann, K. C., & Thayer, C. W. (1996). Sr/Ca and $^{13}\text{C}/^{12}\text{C}$ ratios in skeletal calcite of *Mytilus trossulus*: covariation with metabolic rate, salinity and carbon isotopic composition of seawater. *Geochemica Cosmochemica Acta*, 60, 4207–4221.
- Lautensach, H. (1967). *Geografía de España y Portugal*. Barcelona: Vicens Vives 814 pp..
- Lopez Bermudez, F., Calvo, F., & Morales, A. (1986). *Geografía de la región de Murcia*. Barcelona: Ketr-es.
- López, S., Turón, X., Montero, E., Palacín, C., Duarte, C. M., & Tarjuelo, I. (1998). Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinoidea). Interannual variability and plankton-benthos coupling. *Marine Ecology Progress Series*, 172, 239–251.
- Maheras, P. (1988). Changes in precipitation conditions in the Western Mediterranean over the last century. *Journal of Climatology*, 8, 179–189.
- Marbà, N., & Duarte, C. M. (1994). Growth response of the seagrass *Cymodocea nodosa* to experimental burial and erosion. *Marine Ecology Progress Series*, 107, 307–311.
- Marbà, N., & Duarte, C. M. (1997). Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral. *Limnology and Oceanography*, 42, 800–810.
- Marbà, N., Cebrián, J., Enríquez, S., & Duarte, C. M. (1996a). Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. *Marine Ecology Progress Series*, 133, 203–215.
- Marbà, N., Duarte, C. M., Cebrián, J., Enríquez, S., Gallegos, M. E., Olesen, B., & Sand-Jensen, K. (1996b). Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. *Marine Ecology Progress Series*, 137, 203–213.
- Marchetti, R. (1992). The problem of the Emilia Romagna coastal waters: facts and interpretation. In R. A. Vollenwider, R. Marchetti, & R. Viviani, *Marine Coastal Eutrophication. Science of the total Environment Suppl* (pp. 21–33).
- Martin, J.-M., & Milliman, J. D. (1997). EROS 2000 (European River Ocean System). The western Mediterranean: an introduction. *Deep-Sea Research II*, 44, 3–4.
- Mateo, M. A., Romero, J., Pérez, M., Littler, M. M., & Littler, D. S. (1997). Dynamics of millenary

- organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuarine, Coastal and Shelf Science*, 44, 103–110.
- Mazzarella, A., & Palumbo, A. (1988). Long-period variations of mean sea level in the Mediterranean area. *Bollettino di Oceanologia Teorica ed Applicata*, 6, 253–259.
- Mazzarella, A., & Palumbo, A. (1989). Recent changes of mean sea level in the Mediterranean area. *Bollettino di Oceanologia Teorica ed Applicata*, 7, 285–293.
- Mazzocchi, M. G., & Ribera D'Alcala, M. (1995). Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES Journal of Marine Science*, 52, 679–691.
- McConnaughey, T. A., Burdett, J., Whelan, J. F., & Paull, C. K. (1997). Carbon isotopes in biological carbonates: respiration and photosynthesis. *Geochimica Cosmochimica Acta*, 61, 611–622.
- Meade, R. H., & Emery, K. O. (1971). Sea level as affected by river runoff, eastern United States. *Science*, 173, 425–427.
- Metaxas, D. A., Bartzokas, A., & Vitsas, A. (1991). Temperature fluctuations in the Mediterranean area during the last 120 years. *International Journal of Climatology*, 11, 897–908.
- Milliman, J. D. (1992). Sea-level rise response to climatic change and tectonics in the Mediterranean Sea. In L. Jeftic, J. D. Milliman, & G. Sestini, *Climate change in the Mediterranean* (pp. 45–56). (London).
- Modigh, M., Saggiomo, V., & Ribera D'Alcala, M. (1996). Conservative features of picoplankton in a Mediterranean eutrophic area, the Bay of Naples. *Journal of Plankton Research*, 18, 87–95.
- Mura, M. P. (1997). *Dynamics of phytoplankton communities and specific growth rates*. Ph.D. thesis, Universidad Politécnic de Catalunya, Barcelona. (168 pp).
- Mura, M. P., Agustí, S., Cebrián, J., & Satta P. (1996a). Seasonal variation of phytoplankton biomass and community composition in Blanes Bay (1992–1994). In C. M. Duarte, *Seasonality in the Blanes Bay: a paradigm of the northwest Mediterranean littoral*. *Publicación Especial*, (pp.21–30) vol. 22. Instituto Español de Oceanografía.
- Mura, M. P., Agustí, S., Del Girogio, P., Gasol, J., Vaqué, D., & Duarte, C. M. (1996b). Loss-controlled phytoplankton production in nutrient-poor littoral waters of the NW Mediterranean: in situ experimental evidence. *Marine Ecology Progress Series*, 130, 213–219.
- Palomera, I., & Olivar, M. P. (1996). Nearshore ichthyoplankton off the Costa Brava (Northwest Mediterranean). In C. M. Duarte, *Seasonality in the Blanes Bay: a paradigm of the northwest Mediterranean littoral*. *Publicación Especial*, (47–54) vol. 22. Instituto Español de Oceanografía.
- Pauly, D., Christensen, V., Dalsgaard, F., Froese, R., & Torres, T. Jr. (1998). Fishing down marine food webs. *Science*, 279, 860–863.
- Pergent, G., & Pergent-Martini, C. (1990). Some applications of lepidochronological analysis in the seagrass *Posidonia oceanica*. *Botanica Marina*, 33, 299–310.
- Peterson, R. G., Stramma, L., & Kortum, G. (1996). Early concept and charts of ocean circulation. *Progress in Oceanography*, 37, 1–115.
- Prairie, Y.-T., & Duarte, C. M. (1996). Weak density-dependence and ecosystem noise as determinants of phytoplankton temporal dynamics. *Ecoscience*, 3, 451–460.
- Richardson, C. A., Kennedy, H. A., Duarte, C. M., Kennedy, D. P., & Proud, S. V. (1999). Population density and growth of the fan mussel, *Pinna nobilis* from SE Spanish Mediterranean seagrass, *Posidonia oceanica*, meadows. *Marine Biology*, 133, 205–212.
- Roether, W., Manca, B. B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., Kovacevic, V., & Luchetta, A. (1996). Recent changes in Eastern Mediterranean deep waters. *Science*, 271, 333–335.
- Rohling, E. J., & Bryden, H. L. (1992). Man-induced salinity and temperature increases in Western Mediterranean deep water. *Journal of Geophysical Research*, 97C, 11191–11198.
- Sand-Jensen, K., & Borum, J. (1991). Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany*, 41, 137–175.
- Sashamanoglou, H. S., & Makrogiannis, T. J. (1992). Temperature trends over the Mediterranean Region, 1950–88. *Theoretical and Applied Climatology*, 45, 183–192.
- Satta, M. P., Agustí, S., Mura M. P., & Duarte, C. M. (1996). Gross planktonic primary production in the Bay of Blanes (1992–1994). In C. M. Duarte, *Seasonality in the Blanes Bay: a paradigm of the northwest Mediterranean littoral*. *Publicación Especial*, (pp. 31–38) vol. 22. Instituto Español de Oceanografía
- Scotto Di Carlo, R., Tomas, C. R., Ianora, A., Marino, D., Mazzocchi, M. G., Modigh, M., Montresor,

- M., Petrillo, L., Ribera D'Alcala, M., Saggiomo, V., & Zingone, A. (1985). Uno estudio integrato dell'ecosistema pelagico costiero del Golfo di Napoli. *Nova Thalassia*, 7, 99–128.
- Sestini, G. (1989). The impact of sea level rise on low lying Mediterranean coasts. *Bollettino di Oceanologia Teorica ed Applicata*, 7, 295–299.
- Šolić, M., Krstulović, N., Marasović, I., Baranović, A., Pucher-Petković, T., & Vucetić, T. (1997). Analysis of time series of planktonic communities in the Adriatic Sea: distinguishing between natural and man-induced changes. *Oceanologica Acta*, 20, 131–143.
- Strahler, A. N. (1981). *Geografía física*. Barcelona: Omega 767 pp..
- Tanaka, N., Monaghan, M. C., & Rye, D. M. (1986). Contribution of metabolic carbon to mollusc and barnacle shell carbonate. *Nature, London*, 320, 520–522.
- Tsimplis, M. N. (1995). The response of sea level to atmospheric forcing in the Mediterranean. *Journal of Coastal Research*, 11, 1309–1321.
- UNEP (1989). State of the Mediterranean marine environment. *MAP Technical Report Series*, (Vol. 28), (225 pp) Athens.
- Vaqué, D., Blough, H. A., & Duarte, C. M. (1997). Dynamics of ciliate biomass and community structure in an oligotrophic coastal environment (NW Mediterranean). *Aquatic Microbial Ecology*, 12, 71–83.
- Vidondo, B., & Duarte, C. M. (1995). Seasonal growth of *Codium bursa*, a slow-growing Mediterranean macroalga: in situ experimental evidence of nutrient limitation. *Marine Ecology Progress Series*, 123, 185–191.
- Vidondo, B., & Duarte, C. M. (1998). Population structure, dynamics and production of the Mediterranean macroalga *Codium bursa* (Chlorophyceae). *Journal of Phycology*, 34, 918–924.
- Zingone, A., Cassotti, R., Ribera D'Alcala, M., Scardi, M., & Marino, D. (1995). 'St. Martin's summer': the case of an autumn phytoplankton bloom. *Journal of Plankton Research*, 17, 575–593.