

REVIEW

Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea

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ABSTRACT: The Catalan Sea, located between the eastern Iberian coast and the Balearic Islands, is a representative portion of the western Mediterranean basin and provides a valuable case study for climate change effects on Mediterranean ecosystems. Global warming is reflected regionally by a rise in sea level over the last century, an increase in surface temperature of around 1.1°C in the last 35 yr, a progressive salinisation of intermediate and deep waters and a strengthening of the stratification. A likely scenario of what we can expect in the Mediterranean Sea is a considerable decrease in rainfall and wind, warmer surface waters and a prolonged stratification period. The effects on Mediterranean ecosystems are evident in: (1) a meridionalisation of the algal, invertebrate and vertebrate species, which favours the more thermophilic species over the temperate species; (2) mass mortality events of sessile invertebrates of the coralligenous communities owing to anomalous warm waters during the period when food is scarce; (3) increases in the smallest phytoplankton due to the prolongation of the water stratification period; (4) proliferation of gelatinous carnivores, including jellyfish, due to the temperature rise and the lack of rainfall; (5) a faster acidification of seawater, compared with the global oceans, accompanied by a decrease in the capacity to absorb atmospheric CO₂. In order to anticipate and mitigate these predicted changes, we recommend investing in research and observation, conserving areas that serve as indicators of climate change and reducing other anthropogenic pressures such as habitat destruction, over-fishing or pollution, which may act synergistically to accelerate these changes.

KEY WORDS: Climate change · Marine ecosystems · Catalan Sea · Mediterranean Sea · Time series

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1. VULNERABILITY OF MEDITERRANEAN MARINE ECOSYSTEMS TO CLIMATE CHANGE

The effects of climate change associated with human activity are starting to be detected in marine ecosystems of all the world's oceans (Hoegh-Guldberg & Bruno 2010). The wide range of processes that are affected by climate change (e.g. meteorological, chemical, biological), however, make it very difficult to predict the magnitude and rate of its

effects. Only an extensive knowledge of how the system operates will allow us to understand, interpret and predict the consequences of climate change. However, there is still very little information available on marine ecosystems, far less than there is on land ecosystems, which is mainly due to the obvious difficulties involved in studying the sea.

Several distinctive features make the Mediterranean Sea particularly sensitive to climate change. The Mediterranean Sea has only a narrow connec-

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tion with the Atlantic Ocean through the Strait of Gibraltar, an artificial connection with the Red Sea through the Suez Canal and a connection with the Black Sea through the Bosphorus Strait. The hot dry summers and scarcity of river inputs make the Mediterranean Sea a concentration basin. During winter, the intense cooling and evaporation of Atlantic surface water increase its density, which causes this water to sink in the northern parts of both the western and eastern Mediterranean basins. In the eastern basin, the formation of Levantine Intermediate Water (at ~300 to 400 m) plays an important role in the functioning of the whole Mediterranean Sea, as it is involved in the formation of deep waters in the Aegean Sea, the Adriatic Sea, the Tyrrhenian Sea and the Gulf of Lion (Millot & Taupier-Letage 2005). The small size of the Mediterranean Sea also suggests that the impact and rate of climate change will be large and rapid. The average water depth is around 1500 m, and the renewal rate of deep water is relatively fast, between 15 and 50 yr (Bethoux et al. 2002, 2005), compared with that of the world's oceans (from centuries to millennia for the North Atlantic and world oceans, respectively, Broecker 1979, 1980). Heat and CO₂ penetration is therefore very rapid (Rixen et al. 2005, Touratier & Goyet 2009), and the effects of these changes on marine organisms may become apparent rather quickly.

Another characteristic of the Mediterranean Sea is its oligotrophy, i.e. its very low availability of macronutrients (nitrate, phosphate, silicate) in the surface waters. This is because the Mediterranean Sea receives Atlantic surface waters (poor in nutrients) through the Strait of Gibraltar, while it exports, through this strait, deep Mediterranean water rich in remineralized nutrients. This makes the Mediterranean Sea a nutrient-poor system with limited productivity. Within this context of oligotrophy, the mesoscale phenomena (fronts and divergences) of the western basin lead to considerable regional fertilisation. The degree of oligotrophy gradually increases from the western to the eastern basin, comparable with the productivity gradient, which is 3.3 times lower in the eastern basin (Krom et al. 1991, Turley et al. 2000). These differences in productivity lead to varying diversity and quantity in fishery production and the biomass of benthic organisms (Danovaro et al. 1999).

The Mediterranean Sea also contains high biological diversity. Although it occupies only 0.82% of the global ocean surface, it contains 6.3% of all described marine macrophyte and metazoan species (Coll et al. 2010). Within the Mediterranean Sea, 67% of the species are found in the western basin.

Currently, the mean percentage of native species is 20.2%. The highest proportions of endemism are found in sponges (48%), ascidians (35%), echinoderms (23%), bryozoans (23%), macrophytobenthic species (22%) and fishes (12%). Changes in climate exert a central role on marine species (Hawkins et al. 2003) because they cause direct effects on the organisms and their biotic interactions. Furthermore, the indications for a rapid rate of change in an area with a very high proportion of endemic species (20%) suggest that the potential impact of climate change on the overall diversity of Mediterranean ecosystems could be high. Mediterranean sessile invertebrates may be among the most affected because many of them exhibit limited dispersal abilities (Duran et al. 2004, Blanquer & Uriz 2010, Ledoux et al. 2010, Mokhtar-Jamaï et al. 2011). Mobile taxa such as fishes may be less affected because, although a relatively high degree of population structure has also been observed in some littoral fish species (Carreras-Carbonell et al. 2006), many display differentiation at distances of hundreds to thousands of kilometers and in relation to oceanographic fronts (Patarnello et al. 2007, Galarza et al. 2009). However, risk of extinction has been identified in motile species dwelling in highly fragmented habitats (Lejeusne & Chevaldonné 2006).

At the same time, large scale climatic variability is one of the most determinant factors of the availability of resources for marine ecosystems. In the Mediterranean Sea, the interannual temperature, wind patterns and rainfall regimes are affected by the Atlantic climate, which can be represented by a recurrent pattern of climate variability known as the North Atlantic Oscillation (NAO). Although the NAO index has been used widely in Europe, other regional indices have been developed for the Mediterranean given that the NAO only weakly explains the climate variability over this sea. The Mediterranean Oscillation (MO) relates to the difference in pressures between the North Atlantic Ocean and the southeastern Mediterranean Sea (Supić et al. 2004) and the Western Mediterranean Oscillation (WeMO) is defined from the difference in pressures between San Fernando (south of Spain) and Padua, Italy (Martin-Vide & Lopez-Bustins 2006). The WeMO index explains the rainfall events in autumn and winter (López-Bustins et al. 2008) better than does the NAO. As there are few time series of data that are long enough, the connections observed between ecosystem dynamics and medium-term climate variability are the best indicators for understanding the responses to global warming at larger scales.

Climate change is by no means the only cause of transformation in Mediterranean coastal ecosystems. There are many intense anthropogenic pressures: overfishing, habitat destruction, increased abundance of alien species, alteration of rivers inflow and pollution (Ballesteros 2006, Klein & Verlaque 2008, Coma et al. 2011). At present, habitat destruction is considered the main threat for a wide variety of taxonomic groups in the Mediterranean. However, climate change is predicted to become progressively more important (Ballesteros 2006, Coll et al. 2010) due to the inertia of the phenomenon and the risk of exceeding several thresholds (Rockström et al. 2009). Potential synergies with these additional stressors are still largely unknown.

In the present study, we focus on the Catalan Sea (northwestern Mediterranean), defined by the eastern Iberian coast north of Cape La Nau and the Balearic Islands (Fig. 1). Whilst most of the Mediterranean Sea is oligotrophic, this is a relatively productive area (Estrada & Margalef 1988). The Catalan Sea presents a cyclonic circulation with a permanent southwestward current, the Northern Current (also known as the Liguro–Provençal–Catalan Current), which flows from the Ligurian Sea (off northwest Italy) to the Catalan Sea and follows the continental slope. In the Channel of Ibiza, the Northern Current splits and one branch flows eastward along the Balearic Islands (Castellón et al. 1990) forming the Balearic front that separates the central waters of the Catalan Sea from modified Atlantic waters (Font et al. 1988).

In the following sections we first describe the most characteristic trends in the evolution of particular marine physicochemical variables and discuss the existence of significant changes in recent decades and their relationship to global climate change. We

then select some communities and ecosystems that we consider are most representative or have the largest ecological, social and economic impact in the area of study. For each of these systems, we first present the evidence of changes in them that have occurred as a result of climate change, and then highlight the most likely future trends for organisms in these systems in the Catalan Sea.

2. THE GEOPHYSICAL ENVIRONMENT: IS THERE EVIDENCE OF CHANGE?

To detect changes in the marine environment and be able to quantify their magnitude, it is necessary to have time series of key physicochemical parameters (e.g. temperature, salinity). Only then, by analysing statistically the variability over time, are we able to provide evidence for the existence of changes. Although there is a considerable network of meteorological stations on the land, comparatively little data exist for seas and oceans, which is mainly due to logistical difficulties in establishing a similar network in this environment. In the following section, we briefly recapitulate the evolution of seawater temperature, sea level, salinity, stability of the water column, seawater acidification and marine currents as well as wave and storm frequency in the Catalan Sea (see also Table 1).

2.1. Seawater temperature

On a global scale, as stated in the latest report of the Intergovernmental Panel on Climate Change (IPCC), ocean surface temperatures have increased, on average, by around 0.7°C since the beginning of the 20th century (Trenberth et al. 2007). Climate model projections for the 21st century indicate even larger increases.

Time series data on the coastal Catalan Sea have been gathered since 1969, and without interruptions since 1974 at L'Estartit. 'L'Estartit station', which is over 90 m deep, is located 4 km from the harbour of L'Estartit, Girona, Spain, and 1.7 km east of the Medes Islands (42° 03' N, 3° 15' 15" E; Fig. 1). At this site, sea temperature is measured weekly at several depths from the surface to 80 m. Measurement of salinity and sea level, among other variables, commenced more recently (Salat & Pascual 2002, 2006). This valuable time series from L'Estartit station shows clear intra- and interannual variability of several variables. Over the past 35 yr, a trend of increas-



Fig. 1. Western Mediterranean Sea. Stars: oceanographic stations

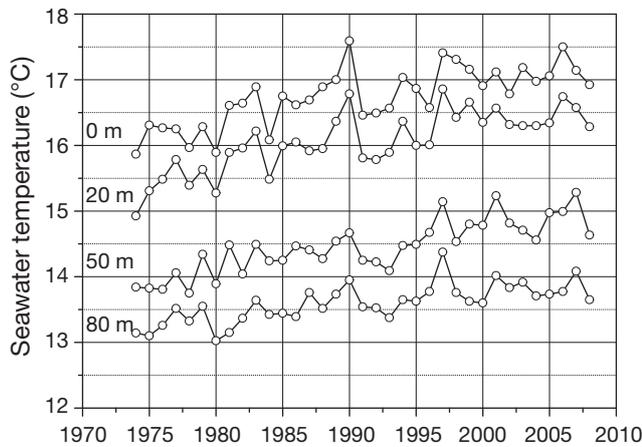


Fig. 2. Evolution over time of the mean annual sea temperatures at L'Estartit station from 1974 to 2008. From top to bottom of graph curves represent 0, 20, 50 and 80 m depth, respectively

ing water temperature can be seen very clearly at all depths studied (Fig. 2, Table 1).

Other datasets also depict this increasing trend in temperature over the last decades. For example, climatological analyses of temperature data from the Mediterranean show an increase of around 0.5°C in the first 150 m of the water column between 1985 and 2000 (Rixen et al. 2005). At L'Estartit station, temperatures have increased around 1.1°C in the uppermost waters (0 to 50m) and around 0.7°C at 80 m over the last 35 yr (Figs. 2 & 3, Table 1), which is a similar rate to that inferred from satellite observations between 1985 and 2006 for the western Mediterranean ($0.03^{\circ}\text{C yr}^{-1}$, Nykjaer 2009). The change in temperature in the northwestern Mediterranean Sea in the

last decades seems to be more pronounced than the temperature increase in the oceans on a global scale. A recent compilation of temperature time series from the western Mediterranean Sea, which also includes L'Estartit station, reveals a consistent warming pattern over the last 40 yr at a very similar increasing rate (Vargas-Yáñez et al. 2010).

As we describe in the following sections, the temperature increases are critical for many species and marine ecosystems (Table A1 in the Appendix) and lead to, for example, changes in the biogeography of native species, incorporations of new species, mass mortality events in fragile ecosystems and changes in the ecosystem's metabolism and services.

2.2. Sea level

On a global scale, the sea level increased by approximately 1.7 to 1.8 mm yr^{-1} between 1961 and 2003 (Bindoff et al. 2007) and by 3.3 mm yr^{-1} between 1993 and 2007 (Cazenave & Llovel 2010). According to the fourth IPCC report, climate model projections indicate similar or greater increases leading to a rise in sea level of 0.18 to 0.59 m in the period between 1980–1999 and 2090–2099 (Meehl et al. 2007). However, this value may actually be a lower limit as the IPCC AR4 projections do not consider certain instabilities of continental ice associated with coastal glaciers. Recent studies that take these instabilities into account suggest that there will be sea level rises of 0.5 to 1.2 m by the end of this century (Rahmstorf 2007, Cazenave & Llovel 2010).

Table 1. Evidence of change on the geophysical environment at selected locations in the Mediterranean Sea. (–) Data not available

Geophysical variable	Location	Time period	Depth	Change	Mean rate of change (yr^{-1})	Reference
Seawater temperature	Western Mediterranean	1950–2000	Surface–150 m	$+0.3^{\circ}\text{C}$	$+0.006^{\circ}\text{C}$	Rixen et al. (2005)
		1985–2000	Surface–150 m	$+0.5^{\circ}\text{C}$	$+0.033^{\circ}\text{C}$	Rixen et al. (2005)
	L'Estartit	1974–2008	Surface–50 m	$+1.1^{\circ}\text{C}$	$+0.032^{\circ}\text{C}$	Present study
			80 m	$+0.7^{\circ}\text{C}$	$+0.021^{\circ}\text{C}$	Present study
Western Mediterranean	1985–2006	Surface	$+0.6^{\circ}\text{C}$	$+0.029^{\circ}\text{C}$	Nykjaer (2009)	
Sea level	L'Estartit	1990–2009	Surface	$+6.5 \text{ cm}$	$+3.4 \text{ mm}$	Vargas-Yáñez et al. (2008); present study
Salinity	Western Mediterranean	1950–2000	Surface–bottom	$+0.035$ to 0.04 psu	0.0008 psu	Rixen et al. (2005)
Stability of the water column ^a	L'Estartit	1974–2006	Surface–80 m	from 75 to 164 d	$+1.25 \text{ d}$	Coma et al. (2009)
Acidification	Western Mediterranean	Preindustrial to 2001	Surface–bottom	-0.14 to -0.1 pH units	–	Touratier & Goyet (2011)
Currents, waves and storm frequency	Catalan Sea	1984–2007	–	Limited or inconclusive data	–	Sánchez-Arcilla et al. (2008)

^aPeriod in which 20 m water temperature is $>18^{\circ}\text{C}$

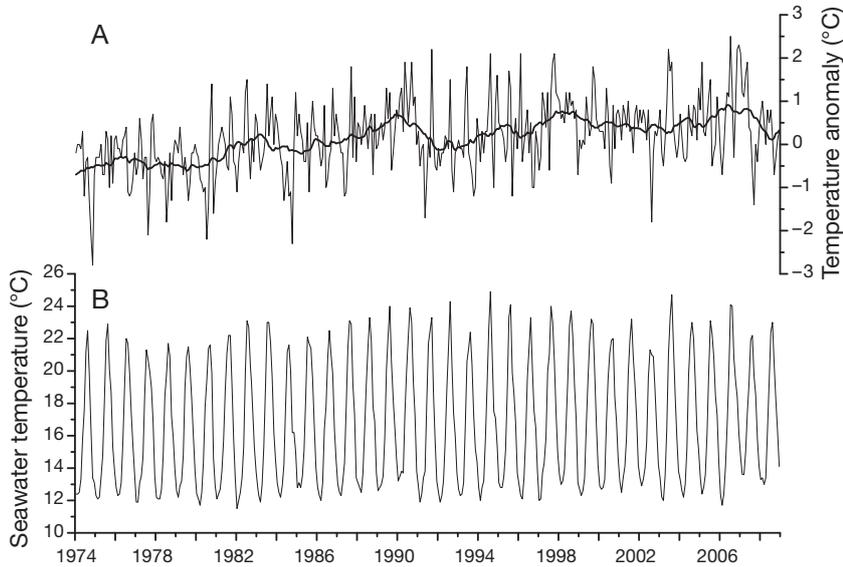


Fig. 3. Instrument records of the sea surface temperature at L'Estartit station for the period from 1974 to 2008. (A) Temperature anomalies calculated according to the difference between each monthly mean of the time series and the climatological monthly mean calculated for the entire period. The thicker line represents the data smoothed with a 24 mo moving average. (B) Monthly mean

Reconstructions based on archaeological evidence show that the level of the Mediterranean Sea has remained roughly the same over the last 2000 yr, and only began to rise significantly in the last 100 yr (Lambeck et al. 2004, Sivan et al. 2004). This change coincides with the increase in temperature associated with global climate change.

The sea level values registered at the L'Estartit harbour since 1990 show an increase of 3.4 mm yr^{-1} since 1990 (Fig. 4, see also Vargas-Yáñez et al. 2008). It seems, however, that the Mediterranean Sea level decreased from 1950 to 1990, probably as a result of a prolonged increase in atmospheric pressure (Tsimplis & Josey 2001, Vargas-Yáñez et al. 2007).

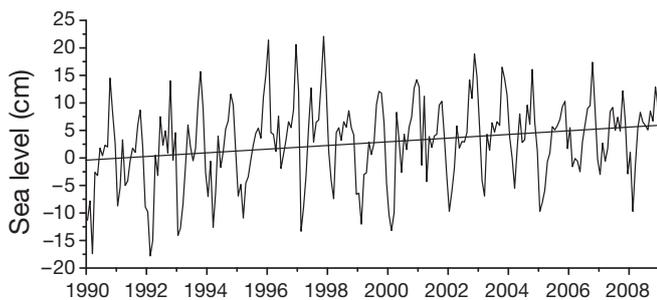


Fig. 4. Instrumental records of sea level at the L'Estartit port for the period from 1990 to 2008. The high resolution curve represents monthly means, and the straight line corresponds to the linear regression, which shows the increasing trend during this period

The rise in global sea level is mainly due to the thermal expansion of water because of warming and increases in water mass due to continental ice melting. However, at a regional scale the atmospheric pressure plays a very important role: high pressures make the sea level fall and low pressures allow it rise (Gomis et al. 2008). The contribution of atmospheric pressure may account for 20 to 50% of the yearly sea level variability (Marcos & Tsimplis 2008). In the Mediterranean Sea, the interannual variation in the atmospheric pressure is influenced by the NAO, which has effects on the sea level in the Mediterranean on a decadal scale (Tsimplis & Josey 2001). A more recent investigation has shown that there is also a large correlation between the variations in sea level in the Mediterranean and the MO (Gomis et al. 2008).

The sea level record from L'Estartit station, together with that from Sete and Nice, is consistent with the long-term record from nearby Marseille, which has data going back to 1885 (Marcos & Tsimplis 2008). However, this record shows some discrepancies with those from the ports of Valencia and Barcelona since 1992 (Mosso et al. 2009). An assessment of the quality of these and other tide-gauge records from the Mediterranean indicates some inconsistencies in the record from Valencia, while the record from Barcelona, besides reflecting the more general trend of the area, also records changes in local conditions (Marcos & Tsimplis 2008).

2.3. Salinity

Some studies point to a recent worldwide decrease in the salinity of the oceans (Antonov et al. 2002). However, these estimations, which are based on a limited number of observations, contain important uncertainties (Bindoff et al. 2007). In the Mediterranean Sea, the present evidence suggests the opposite trend: that is, the gradual salinisation of the water, especially in the intermediate and deep layers (more than 150 m deep) (Rixen et al. 2005, Vargas-Yáñez et al. 2010). This increased salinity seems to be related to the general decrease in rainfall and increase in evaporation in the Mediterranean area, and to the

decrease in river flow to the sea due to the construction of dams and reservoirs (Vargas-Yáñez et al. 2007).

Changes in salinity can be critical for the circulation of ocean currents and the stability of the water column, and therefore the nutrient contribution from the deep layers to the photic zone. Such changes can disturb the structure of the communities of planktonic primary producers and the trophic chains that feed on them (e.g. Learmonth et al. 2006).

2.4. Stability of the water column: vertical mixing and stratification

On a global scale, climate model predictions indicate a progressive stratification of the water column (Sarmiento et al. 1998). At low latitudes, this is due to the increase in sea water temperature, which is more pronounced at the surface than in deeper layers. At high latitudes, however, it seems that the intensification of the water stratification is more related to the increase in rainfall. Both processes increase the floatability of the surface waters, stabilise the water column and make it difficult for surface waters (richer in oxygen but poorer in nutrients) and deep waters (the opposite) to mix vertically. These changes have increased the size of the oligotrophic areas of the Pacific and Atlantic oceans by 15 % from 1998 to 2006 (Polovina et al. 2008), which probably has a relationship with the recently reported decline in phytoplanktonic productivity over the past century (Boyce et al. 2010).

In the Catalan Sea, a recent study shows how stratification has intensified over the last decades (Coma et al. 2009). The data from L'Estartit station indicate that the difference between the surface and deep water temperatures has increased over the last 30 yr (Fig. 5A). In the Catalan Sea, the water column goes through 2 very different periods: a period of thermal homogeneity from December/January to March during which the water column is mixed, and a stratification period from April to November/December during which a large vertical gradient of temperature and density is established (Fig. 6). Analysis of the data from the L'Estartit station time series also shows how the stratification period has lengthened over recent decades (Coma et al. 2009). The length of the stratification period (here defined as the period in which the water temperature at 20 m is over 18°C) increased from 75 to 164 d between 1974 and 2006 with a trend of 1.25 d yr⁻¹ (Fig. 5B). This phenomenon is not related to an increase in the freshwater inflows to the sea but to the increase in temperature (see Section 2.1).

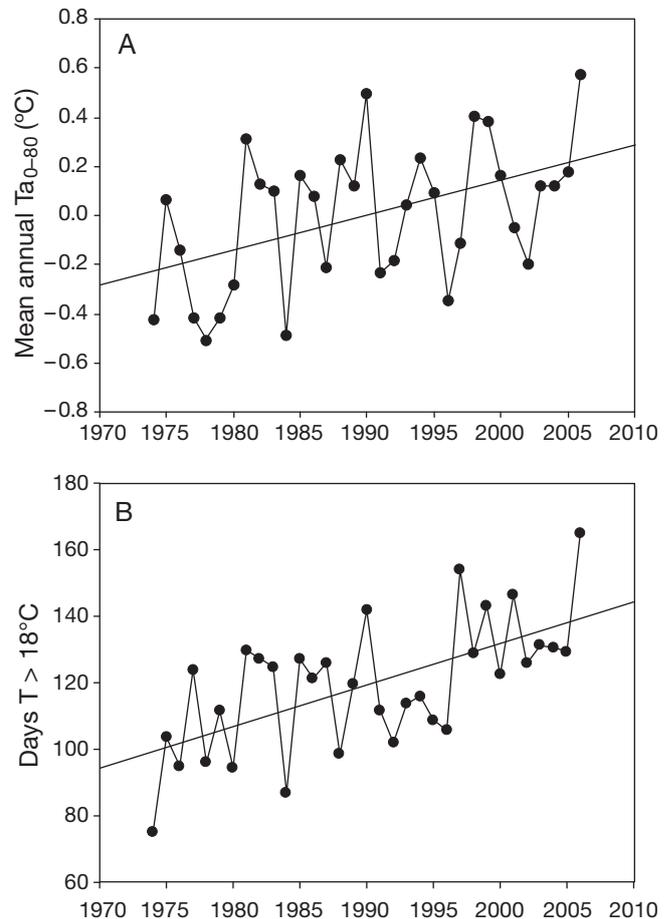


Fig. 5. Trends calculated with the temperature database from the L'Estartit time series for the period from 1974 to 2006 of: (A) the difference in seawater temperature between the surface and 80 m depth (T_{a0-80} , calculated as the anomaly between the difference observed and the mean difference of the entire period); (B) the number of days in each year in which the temperature at 20 m was higher than 18°C, which characterises the water column stratification. Figure is adapted from Coma et al. (2009)

2.5. Acidification of the oceans: the twin of global warming

Together with global warming, the increase in atmospheric CO₂ due to anthropogenic activities is causing a progressive acidification of Earth's seas and oceans owing to the continued oceanic absorption of CO₂. As soon as the CO₂ molecules enter the sea, they participate in a series of chemical equilibria. This translates into (1) an increase in the concentration of hydrogen ions and therefore a decrease in pH, and (2) a decrease in the concentration of carbonate ions, which are the basic components that calcifying organisms, such as corals, mussels, coccolithophores and pteropods, use to build their skeleton

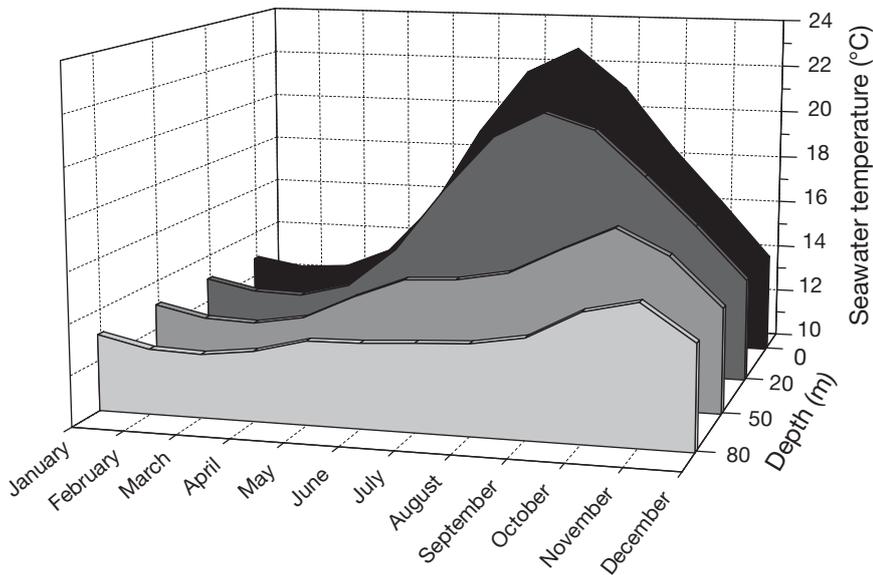


Fig. 6. Annual cycle of monthly mean seawater temperatures at L'Estartit station at 4 different depths (surface and 20, 50 and 80 m) for the period from 1974 to 2008

or structure. These organisms are thus expected to be affected by acidification, as this change would probably impair their growth. The changes in the chemistry of seawater due to dissolved CO_2 generated by anthropogenic activities are large enough to affect other chemical, biological and gas exchange processes. The possible repercussions of the gradual acidification of seas and oceans span from the effects on individual organisms to those on ecosystems and biogeochemical cycles (see reviews in Fabry et al. 2008, Guinotte & Fabry 2008, and Pelejero et al. 2010).

The oceanic pH is calculated to have already decreased an average of 0.1 units (a 30% increase in the proton concentration) relative to preindustrial levels (Raven et al. 2005). The projections of the changes in pH depend on the CO_2 that humans emit to the atmosphere and the time they take to do so (Zeebe et al. 2008). By the end of the 21st century the predicted decrease in pH could be around 0.3 or 0.4 units (Steinacher et al. 2009). Paleoceanographic studies show that changes of this magnitude are unprecedented in at least the last 40 million yr (Pelejero et al. 2010).

The Mediterranean Sea has certain characteristics that make it especially sensitive and vulnerable to changes in atmospheric CO_2 and gradual acidification. The residence time of the Mediterranean deep waters (from 15 to 50 yr in the Algero-Provencal and eastern basins, respectively, Bethoux et al. 2002, 2005) is very short in comparison with the Earth's oceans (Broecker 1979, 1980). This means that the penetration of anthropogenic CO_2 , which could take from centuries to millennia in the Earth's

oceans depending on the region and depth, is much faster in the Mediterranean, resulting in earlier changes. Furthermore, the Mediterranean Sea is saltier and more alkaline than the world's oceans and therefore has a greater capacity to absorb CO_2 . A recent study that quantified the variations in the amount of anthropogenic carbon that has entered the Mediterranean during the last decade (Touratier & Goyet 2009) showed significantly higher CO_2 penetration levels than those found for the North Atlantic Ocean (Vázquez-Rodríguez et al. 2009). These results suggest that the absorption of CO_2 in the Mediterranean Sea, and therefore the acidification of its waters, is occurring more quickly than in the North Atlantic,

where the highest vertically integrated concentrations of anthropogenic CO_2 are found (Sabine et al. 2004). Recently, a first estimation of seawater acidification in the Mediterranean Sea identified a pH decrease of up to 0.14 units in the western Mediterranean Sea since preindustrial times (Touratier & Goyet 2011), which is of higher magnitude than the global surface ocean decrease of ~ 0.1 pH units over this time period. A recent report has also listed fairly exhaustively the possible repercussions of the acidification of the Mediterranean Sea (CIESM 2008b), although research in this area has just started.

2.6. Marine currents, waves and storm frequency

According to the last IPCC report, the frequency of extreme events (heat waves, droughts, floods, hurricanes) on a global scale has increased in recent decades (Trenberth et al. 2007) and is likely to further increase in the future (Meehl et al. 2007). An atmosphere with more carbon dioxide is—due to its warming characteristics—a more energetic atmosphere that has a greater capacity to store water vapour and a higher probability of developing extreme weather. With global warming, the energy of seas and oceans has also increased, which has been related to the increase in the length and intensity of tropical storms and hurricanes recorded since the 1970s (Trenberth et al. 2007). Models predict nearly a doubling of the frequency of force 4 or 5 hurricanes by the end of this century (Bender et al. 2010).

In theory, this intensification of extreme events should also occur in the Mediterranean region, which would translate into more sea storms and intense wave episodes accompanied by the intensification of winds. The limited data from the few available time series, however, do not allow us to discern clear trends in this aspect, even though there have been several severe storm events in the northwestern Mediterranean Sea during the last decades (Sánchez-Arcilla et al. 2008). Curiously, the future projections made so far suggest an easing of storms (Lionello et al. 2008); however, the time series of instrumental wave measurements, all less than 25 yr in length, make it difficult to predict extreme phenomena related to marine dynamics (Sánchez-Arcilla et al. 2008). Nevertheless, an increase in heat waves and droughts (Beniston et al. 2007) as well as an increase in extreme rainfall (López-Moreno & Beniston 2009) seem to be predictable.

Changes in storm intensity and wave events could affect the marine ecosystems associated with sandy and rocky bottoms, which are often physically damaged by wave action, particularly during prolonged episodes of easterly winds, locally known as *levantades*. These events also have an effect over the pelagic ecosystem, which is greatly influenced by external inputs of kinetic energy (Guadayol et al. 2009).

Climate change could also alter the marine circulation patterns of the Mediterranean Sea, which are determined by changes in water density more than by wind effects (Font 1990). The changes in salinity and temperature mentioned previously could therefore lead to alterations in marine currents. Although important changes in the dynamics of marine currents have been described, especially deep currents (see the revision in CIESM 2009), there are still no specific predictions on the changes we can expect for the future. For marine ecosystems, changes in the marine currents could affect, for example, the migration movements of marine species that rely on being carried by the current (CIESM 2009).

3. EFFECTS ON MARINE ORGANISMS

3.1. Planktonic primary producers and heterotrophs

Plankton up to 0.2 mm in size comprise most of the biomass and diversity, carry out virtually all marine primary production and are the base of the food web of the pelagic ecosystem. In addition, they act as a

vehicle to cycle the main elements and are responsible for most of the exchanges of materials between the sea and the atmosphere (Falkowski et al. 1998). It is not possible to understand the effects of climate change on the pelagic ecosystem without understanding its effects on planktonic organisms, both individually and collectively. Unlike the organisms with more collective biomass on land, which have relatively long lives and are closely linked to their place on the land, planktonic organisms have a more ephemeral dynamic as they are located in a moving, changing environment. This is especially relevant for primary producers; the phytoplankton depend on the hydrography, mainly the stability of the water column and how it fluctuates over time (Margalef 1978). These factors not only determine the potential production and biomass, they also determine the size structure, the taxonomic composition, the biogeochemical dynamic and functions of the phytoplankton community. From here, the trophic webs are structured through bacteria that decompose organic material, bacterivorous, herbivorous and carnivorous protists and filter feeders or preying pluricellular organisms.

The impacts of climate on plankton can be direct, such as through the effects of temperature and solar radiation on their physiology and growth substrates, or indirect, through caloric and kinetic energy inputs and freshwater inputs, which determine the availability of essential elements, light and reducing power (Falkowski et al. 1998). In any case, predicting the health of Mediterranean marine ecosystems in response to global warming and other anthropogenic phenomena inevitably leads to understanding and predicting the adaptations of the planktonic community to the changing environment.

3.1.1. Evidence of change

Planktonic primary producers (phytoplankton). Most of the long-standing observations of phytoplankton biomass and species composition in the Mediterranean Sea are from coastal waters, and thus present human disturbances other than climate change that also affect marine ecosystems. Processes like eutrophication through coastal discharges, land mobilization and pollution have a potential to affect phytoplankton development at least as much as climate does, and separating them is a difficult task.

Between the 1970s and 1990s, a steady decrease in the water transparency, indicative of increased phytoplankton biomass, was observed in the Catalan

Sea littoral (Duarte et al. 1999). This pattern, which was consistent with the observed trends in the Adriatic Sea (Solic et al. 1997, Mozeti et al. 2010, Ninčević Gladan et al. 2010), was not attributed to climate change but to the rise of nutrient inputs associated with the increase in the permanent and temporary human population on the coast. Throughout the last decade, however, the time series studies in the Gulf of Naples (Zingone et al. 2010), the Bay of Calvi, Corsica (Goffart et al. 2002), and the Adriatic Sea (Mozeti et al. 2010, Ninčević Gladan et al. 2010) have all shown what seems to be a common decrease in phytoplankton biomass. In semi-enclosed regions like the Adriatic Sea, this decrease has been attributed to reduced eutrophication by lowered nutrient discharges (Mozeti et al. 2010). Conversely, in the Bay of Calvi, which is less productive due to the influence of Atlantic waters and a lower input of external energy (wind) and continental waters, the decrease in the concentration of chlorophyll *a* (chl *a*) at the surface has been steady since the 1970s and has evolved concurrently with the increase in temperature between the 1970s and 1990s (Goffart et al. 2002).

The only time series held in open waters of the western Mediterranean is the DYFAMED station in the Ligurian Sea (Fig. 1). There, an increase in the phytoplankton biomass was observed during the 1990s, as inferred from increased concentrations of chl *a* integrated through the upper 250 m of the water column. This region is characterised by deep-mixing driven by strong winds, which causes light limitation in phytoplankton growth in winter, despite the presence of river-discharged nutrients. A lengthening of the stratification period implies a lengthening of the productive period, because it alleviates light limitation (Marty et al. 2002).

Therefore the sparse data available suggest that the potential effects of climate change on the biomass and productivity of phytoplankton largely depends on the littoral environmental pressure and the existing hydrodynamic regime (Table A1). In near-shore waters, local perturbations on geochemical fluxes have a much greater influence than does climate. In the open sea (off the shelf), 2 hydrodynamic regimes must be differentiated: (1) in the northernmost sector, the productivity of the seasonally strongly mixed waters may be increased due to climate warming as a result of the lengthened stratification period and the consequent alleviation of light limitation; (2) in most of the Catalan Sea, however, the lengthening of the already long-lasting stratification may prolong nutrient-depleted conditions and reduce annual productivity.

Besides the trends in the biomass and bulk activities, it is also important to consider whether there are changes in the phenology (cycles and timing) and structure of the phytoplankton communities. In Calvi Bay, the winter–spring bloom has moved forward from March to January–February, in line with the earlier stratification owing to the increase in temperature and sunny days and the decrease in wind speed (Goffart et al. 2002). In the Ligurian Sea, the above-mentioned increase in biomass is associated with important but variable changes in community structure. During the 1990s, a decrease in diatom abundance was observed together with an increase in the contribution of smaller organisms, nanoflagellates and picophytoplankton (Marty et al. 2002). The causes were most probably an uncompensated increase in new nutrient inputs derived from continental sources that are deficient in silicate (Béthoux et al. 2002). In the 2000s, however, strong convective mixing episodes associated with droughts led to episodic increases in diatom biomass (Marty & Chivavérini 2010). Although both situations resulted in a general increase in productivity, the consequences of community structure shifts are important because the size of primary producers determines the magnitude of carbon export flows both to the sediments (important for the sea's role in absorbing atmospheric CO₂) and the higher trophic levels (important for fisheries and for benthic invertebrates).

On the Catalan Sea coast, the only data that allow long-term comparisons are the data obtained in Blanes Bay, Spain, in the 1950s and 1960s by Margalef (1964) and the recent data collected by Scharek et al. (2007). The comparison shows that, for the largest phytoplankton (chain-forming diatoms and dinoflagellates), the dominant species have not changed; diatoms typical of more northern temperate waters are found in the bloom at the end of winter, and dinoflagellates typical of tropical waters are found at the end of spring and during summer. It is important to highlight, however, that this perception of no change in the large dominant species does not allow us to infer anything about whether there have been changes in the smallest phytoplankton or in the size distribution of the entire community.

Zooplankton. In the Balearic Islands, Fernández de Puelles & Molinero (2008) observed a certain negative correlation between the positive interannual temperature anomalies and the abundance of zooplankton. The high NAO periods coincide with lower zooplankton abundances. In the Ligurian Sea, Molinero et al. (2005) observed phenological changes, possibly due to climatic causes, that affected the

structure of the zooplankton community. They found that the higher NAO phases favour the copepod *Centrophages* and the lower phases favour *Temora*. Molinero et al. (2008b) also suggested that the dominance of the positive phases of the NAO since the 1980s has led to the progressive substitution of copepods by gelatinous zooplankton, because the latter are better filter feeders (more efficient with smaller phytoplankton) and are better adapted to the stability of the water column. This situation is also reinforced by the fact that gelatinous zooplankton also feed on copepods. Conversi et al. (2010) found an increase in zooplankton abundances after 1980, mainly due to the gelatinous component of the assemblages.

Bacterioplankton. An increase in the abundance of bacteria has been observed in the Adriatic Sea (Solic et al. 1997). At the Blanes Bay Microbial Observatory, the bacterial abundance in surface waters for the last 2 decades (1992 to 2009) does not show a clear trend through time (Duarte et al. 1999, www.icm.csic.es/bio/projects/icmicrobis/bbmo/). Also no conclusions can be made about the phenology and composition of the bacterial community because the molecular techniques used for determining the phylogenetic identity of the bacteria and their linkage with the activity in the ecosystem have only just developed over the last 7 to 8 yr.

Community metabolism. 'Community metabolism' can be defined as the balance between production and respiration of the entire plankton community as a whole, which results in a net balance of CO₂ fixation and oxygen production, or CO₂ production and oxygen consumption. Determining community metabolism requires taking continuous oxygen measurements, which can be compared with climatic data, or carrying out bottle incubation experiments to measure primary production and respiration rates, in which the environmental conditions can be manipulated to simulate changes associated with climate.

Experiments that confine and manipulate the plankton community, whether in bottles in the laboratory or in large containers installed in the sea, allow hypotheses to be tested, although extrapolating the results to the natural environment of the communities is problematic. This kind of experimental approach has shown, for example, that the higher trophic levels (small zooplankton) are the most vulnerable to gradual water warming over a few weeks (Petchev et al. 1999). Vázquez-Domínguez et al. (2007) carried out experiments with water from Blanes Bay sampled monthly over an entire year, and observed that with an increase in temperature of 2.5°C, the carbon respiration of the heterotrophic microorgan-

isms increased without increasing their growth efficiency; that is, in warmer waters the plankton consume more oxygen and produce more CO₂. In fact, temperature is a determining factor of community metabolism because, at a physiological level, it accelerates respiration more than photosynthesis. Therefore, global warming directly favours plankton heterotrophy (net CO₂ production). Climate change in the western Mediterranean Sea, with its hydrographical consequences, also seems to lead to a decrease in the export of organic carbon by sedimentation (Marty et al. 2002). Therefore, it also results in more recycling close to the surface by respiration, and thus indirectly accentuates the heterotrophy of the ecosystem. If we take into account that the solubility of CO₂ also decreases with temperature, we see that everything points to a loss in the sea's capacity to absorb the growing quantities of atmospheric CO₂.

3.1.2. Predicted trends

The tendency in the western Mediterranean Sea and the Catalan Sea, as in all the world's oceans, is for the length and intensity of stratification to increase with global warming. The climatic variability associated with the NAO can be used for predicting climate changes. The positive phases of the NAO, which involve higher atmospheric pressures and temperatures, and decreases in rainfall and wind force, favour the warming and stratification of the surface water in the open sea. Warming leads to a decrease in the solubility of CO₂, and the strengthening of the stratification means that fewer nutrients arrive to surface waters (Fig. 7). Although the effect on the annual primary production is not completely clear, it does seem that these hydrographical changes will lead to (1) changes in the structure of the plankton communities and the metabolism of the ecosystem, which will favour the smallest plankton, (2) a relative increase in the respiration with respect to primary production (increase in heterotrophy) and (3) a decrease in the carbon exported to the seafloor and fish (Fig. 7). Overall, all these changes diminish the sea's capacity to absorb atmospheric CO₂.

3.2. Jellyfish on the coast

Jellyfish are gelatinous planktonic heterotrophic organisms present in practically all marine environments of the world. When the conditions are favourable, they form dense swarms of individuals.

In these cases, and understanding that they are very efficient at capturing prey, jellyfish channel a large part of the energy absorbed by the pelagic ecosystem in planktonic secondary production. Jellyfish are important from ecological and evolutionary perspectives, and in terms of their contribution to biodiversity. They are abundant as bycatch in the fishing industry, are a source of obstruction to power plant turbines, and can have a negative effect on tourism at beaches. Moreover, there is evidence that the problem will grow larger with global warming, pollution and overfishing (Purcell et al. 2007). Most of the energy that once circulated through fishes is now processed by other predators (especially Cnidaria and Ctenophora) that fill a gap within the trophic system (Mills 2001). Fishing activity continues to remove large predators and, as a result, carnivorous zooplankton proliferate. Jellyfish and other pelagic cnidarians are consumers of ichthyoplankton (i.e. fish larvae and eggs) in the world's oceans and seas, including the Catalan Sea (Lynam et al. 2005, Sabatés et al. 2010), and thus concentrate in waters where fish reproduce or lay their larvae and eggs (Purcell & Grover 1990). Their presence in high numbers is thus detrimental for fisheries (Brodeur et al. 2002).

In the Catalan Sea coasts, the large jellyfish swarms observed at the beaches and the growing number of swimmers stung by these organisms have set off an alarm signal (Gili et al. 2010). This increase in jellyfish abundance has been discussed widely in the media, which has led to the launch of public health campaigns and environmental monitoring programmes. Unfortunately, systematically documented observations are scarce and relatively recent, which makes it difficult to study the relationship between the jellyfish swarms in local waters and climate change, as has been done in other areas (Purcell et al. 2007). However, the analysis of the existing data, together with the studies carried out in neighbouring regions and those climatically similar to the Catalan Sea, along with the growing knowledge of the life cycle of these organisms, allow us to outline the causes behind the abundance of jellyfish on the Catalan Sea coast and determine the most probable future trends.

3.2.1. Evidence of change

The Zoological Station of Villefranche-sur-Mer, France, has recorded the presence of the jellyfish, *Pelagia noctiluca*, on the coasts of the Ligurian Sea since the end of the 19th century. Combining these data with observations documented in other institu-

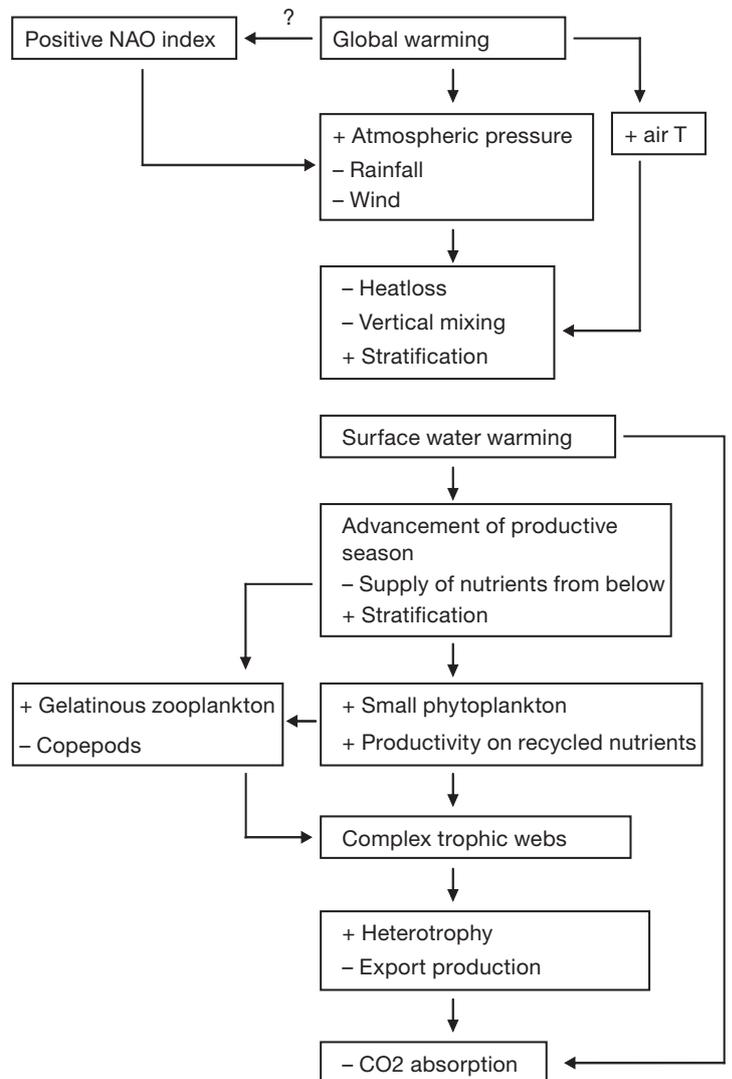


Fig. 7. Mechanisms by which climate change and global warming can affect pelagic ecosystems. The diagram summarises and illustrates graphically the explanation provided in Section 3.1. NAO: North Atlantic Oscillation

tions, it was possible to reconstruct a 200 yr time series (1785 to 1985) of the presence of this species (Goy et al. 1989). The finer analysis of the period from 1875 to 1985 showed a certain cyclic nature in the alternation of years with *Pelagia* and years without *Pelagia*. In fact, the contingency periodogram of this series indicated that approximately every 12 yr there was a period of 2 to 5 consecutive years when jellyfish were present. The comparison with climate data showed that the years with jellyfish coincided with years with little rainfall, high temperatures and high atmospheric pressure from May to August, the reproduction period of *Pelagia* (Goy et al. 1989). In

the last 2 decades, it seems that this alternating tendency with a marked periodicity has been modified and jellyfish intrusions are more frequent. Jellyfish appearance along the Catalan Sea coast shows maxima in abundance every 3 to 4 yr instead of the previously observed 12 yr period (Gili et al. 2010; Fig. 8A). Furthermore, similar observations have been made in areas all over the planet, which suggests that it is a worldwide phenomenon (Purcell et al. 2007). Over the last 5 yr, there has also been a change in the dominant species that proliferate on the coast, with increasing abundance of littoral species like *Rhizostoma pulmo* and the displacement of offshore species like *P. noctiluca* (Fuentes et al. 2011; Fig. 8B). This is because littoral species normally present both an asexual phase (polyp) and a pelagic sexual phase (medusa) while offshore species only present a medusa stage in their life cycle. The polyp phase is believed to benefit from increasing temperatures, which would enhance polyp survival to the medusa stage.

Since 2000, and especially in the last 5 yr, an increase in jellyfish swarms has been observed close to the Catalan Sea coast along with an increase in the duration of the blooms. Moreover, there now appear to be more species that form large swarms. The proliferation of jellyfish on the coasts and beaches depends mainly on 2 factors: (1) the conditions for growth and reproduction in areas far from the coast, where the most abundant species reaching the beaches originate; (2) the transport of the swarms from the open sea and their accumulation close to the coast (Sabatés et al. 2010).

Carnivorous gelatinous organisms are particularly responsive to temperature and climatic oscillations (Molinero et al. 2008a). The increase in temperature positively affects both their growth and reproductive success, which has already been proposed as a direct cause of the increase in jellyfish swarms in other seas (Arai 1997, Brodeur et al. 1999). It also seems to be the reason behind the proliferation in temperate waters of thermophilic species normally associated with subtropical waters. An example of the latter phenomenon is the observation in 2009 for the first time on the Catalan coasts of the ctenophore, *Mnemiopsis leidyi* (Fuentes et al. 2009). The success of introduced *M. leidyi* has been attributed mainly to the reduced competition due to overfished populations of zooplanktivorous fish and the lack of predators (Siapatis et al. 2008). The proliferation of other important invasive species such the cubemedusa *Carybdea marsupialis* in the western Mediterranean Sea have been related to the increase of water tem-

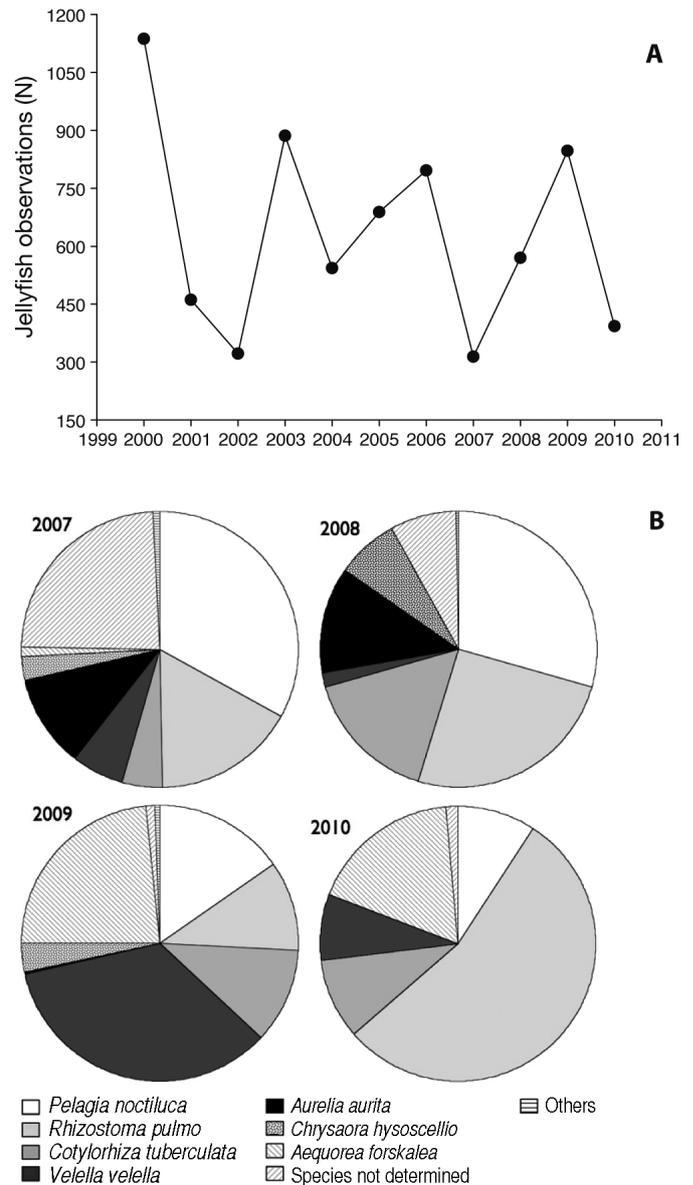


Fig. 8. (A) Total number of jellyfish observations on the Catalan coast from 1999 to 2011. 'Observation' indicates the presence of jellyfish blooms with more than 3 individuals m^{-2} . The frequency and location of sightings were constant over the period of study, with a total of 15 000 sightings during the summer months. (B) Distribution of the different species of jellies detected on the Catalan coast between 2007 and 2010

perature and to the increased chances for polyp settlement in artificial substrata such as new small tourist harbours (Bordehore et al. 2011).

However, as mentioned previously, the physiological effects of temperature by itself do not explain the increase in the jellyfish swarms on the beaches and coasts during summer months. While it is true that, owing to the reproductive cycle, the blooms of most

jellyfish reach maximum abundance between the beginning of spring and the end of summer, these abundance peaks are located about 30 to 60 km (20 to 40 miles) from the coast on the limit of the continental shelf. In these areas, hydrographic conditions favour relatively higher plankton production than in the neighbouring, more-stratified, nutrient-poor waters. In fact, in deep waters of the Ligurian Sea an increase in gelatinous plankton has been observed since the 1980s, without the copepods and chaetognaths having increased proportionally (Molinero et al. 2008b, Conversi et al. 2010). For jellyfish swarms to reach the beaches there needs to be transport from the open sea. During the day, jellyfish are situated in deep layers of the water column where they find more food and avoid visual predators; at night they rise up to the surface. The evening sea breezes push the jellyfish towards the coast and beaches, mainly in the summer. Therefore, the period of maximum abundance coincides with the period of maximum intensity of the breezes (Zavodnik 1987).

There is another climatic phenomenon that favours coastal swarms of jellyfish. In the spring and summer, freshwater inputs from rivers and aquifers lower the salinity and temperature, and therefore the density, of the coastal water. The water density becomes discontinuous, which makes it difficult for surface water, and therefore jellyfish, from the open sea to reach the coast (J. M. Gili unpubl. data). The gradual warming of the Mediterranean climate involves a warming of the shallow coastal waters in spring and summer, and the decrease in the rainfall means that the freshwater inputs are increasingly scarce. This leads to the early homogenisation of the coastal waters with water from the open sea, which facilitates the wind action and the arrival of jellyfish to the coast.

3.2.2. Predicted trends

There is little quantitative data for past or present jellyfish populations. However, as the quality of the data improves, and jelly species are correctly identified, we will see a more accurate view of the response of gelatinous plankton populations to climate change. However, some studies and observations already point to likely future trends. A study by Molinero et al. (2008a) shows that positive phases of the NAO favour jellyfish blooms in the northwestern Mediterranean Sea. These periods have higher temperatures and atmospheric pressures, as well as a lower rainfall (and therefore less river discharge) and

wind force (Lloret et al. 2001). Together these factors promote surface warming and stratification in the open sea, the development of gelatinous carnivores and their transport towards the coast (Fig. 7). This climatic trend, along with the fact that other anthropogenic pressures (see Section 4) are also unlikely to decrease, points to a progressive increase in the presence of jellyfish swarms on the Catalan Sea coast over the upcoming years.

3.3. The Mediterranean coralligenous community

The coralligenous community is a structure of biogenic origin produced by the accumulation of encrusting algae in low light conditions. The animal communities in the coralligenous assemblages vary according to light, currents, sedimentation processes and temperature. In the more eutrophic areas such as the northwestern Mediterranean Sea, gorgonian corals dominate the community together with a wide range of other suspension feeders such as sponges, bryozoans and ascidians. The coralligenous community is symbolic of the Mediterranean, and is highly appreciated by the diving tourism industry. It is biologically important because of its high species diversity (up to 1666 species, Ballesteros 2006) and the great structural complexity created by some of the main building species (encrusting algae, gorgonians and sponges). This complexity contributes decisively to maintaining the biological diversity. However, it is a very vulnerable community, due to the longevity and low turnover of most of the species that constitute it, especially the building species (Coma et al. 1998, Garrabou et al. 2002). These characteristics lead to slow growth and low recruitment, greatly reducing the capacity of the community to recuperate when it undergoes disturbances.

3.3.1. Evidence of change

In recent years, global warming has severely affected marine benthic ecosystems through epidemic diseases and mass mortalities of the organisms (Harvell et al. 1999). The alarm signal sounded in the coral reef ecosystems during the severe coral bleaching events in 1997 and 1998 (Harvell et al. 2002). Recently, both the physical and biological evidence that has accumulated shows that the Mediterranean Sea is suffering the effects of global warming (Table A1). During the summer of 1999, there was a mass mortality event of invertebrates that affected

more than 500 km of the northwestern Mediterranean coastline between Italy and France as well as the north coast of Menorca (Perez et al. 2000, Coma et al. 2006). Another mass mortality event with the same characteristics as that of 1999, but with a larger geographic extension, occurred at the end of the summer of 2003, again in the northwestern Mediterranean. In this case the affected area was several thousand kilometres of coastline from the Gulf of Naples to the Catalan Sea, including Corsica and Sardinia, the Gulf of Genoa, the Provençal coast and the Balearic Islands (Garrabou et al. 2009). In both events the populations of sessile invertebrate suspension feeders of the coralligenous community between 0 and 35 to 45 m depth were the most affected, especially the gorgonian and sponge populations (Table 2). The colonial nature of most of these species means that they can suffer partial mortality, while the colony still survives. This capacity has attenuated the effect of mass mortality events on populations. Nevertheless, in many areas the losses have been approximately 50% of the gorgonian populations (Linares et al. 2005, Coma et al. 2006) and up to 95% for some sponge populations (Maldonado et al. 2010, Cebrian et al. 2011). Evidence of increased recruitment after an event has been observed in some populations indicating that clear-cut restoration trends may occur (a self-thinning process, the reduced population favouring the survival of recruits by decreasing intraspecific competition; Linares et al. 2008a, Cupido et al. 2009) if mass mortality events do not occur frequently. However, if these events do become frequent, the effect in decreasing gonadal output of colonies (Linares et al. 2008b), limiting dispersal (Ledoux et al. 2010, Blanquer & Uriz 2010, Mokhtar-Jamaï et al. 2011) and fragmenting of populations may drive the population to a threshold where persistent population decline occurs (Linares 2010).

The causes of the mass mortalities of invertebrates are related to climate change and its effects. Some hypotheses on the triggering mechanisms have been proposed (Cerrano et al. 2000, Romano et al. 2000, Coma & Ribes 2003, Bally & Garrabou 2007, Torrents et al. 2008, Coma et al. 2009, Bensoussan et al. 2010, Lejeusne et al. 2010, Vezzulli et al. 2010) and include: (1) organisms being exposed to temperatures above the thermal tolerance level of the species, (2) organisms being exposed to temperatures under their critical temperatures, but which still cause physiological stress, and (3) increase in the virulence of pathogenic microorganisms. The mass mortality events have not been characterised by physiologically critical temperatures, although we cannot completely dismiss

this possibility, as critically high temperatures could have occurred locally. Concerning the hypothesis of virulent microorganisms, even though microorganisms have been found (Bally & Garrabou 2007), they have been identified as opportunistic (Cerrano et al. 2000, Martin et al. 2002, Vezzulli et al. 2010). The temperatures at the end of summer during these events were 3 to 4°C above the average and there was a stable water column that would have delayed the vertical mixing that usually occurs at the end of summer and beginning of autumn. These conditions are not critical for the organisms, but can cause physiological stress.

Recently, laboratory experiments and field observations have demonstrated that climate anomalies of extreme stratification are one of the main causes of mortality events of certain invertebrate suspension feeder species of the coralligenous community (Coma et al. 2009). The mechanism that triggers death is physiological stress due to energetic limitations. Summer is energetically unfavourable for these organisms, due to the high temperatures demanding increased respiration, and low food availability, which does not allow them to feed sufficiently to meet this high respiratory demand, causing the organisms to irreversibly lose biomass. The organisms are able to support a 'normal' duration of energetically adverse conditions during summer, but not an abnormal extension of these conditions, particularly if this extension occurs in combination with unusually high temperatures. Mass mortality events occurred in years of prolonged conditions of the period of strong stratification of the water column (Coma et al. 2009). Short periods of unusually high temperatures have been suggested recently as the possible triggering factor of sponge diseases (*Ircinia* spp., Maldonado et al. 2010, Cebrian et al. 2011). However, little is known about how these pathogens will be affected by the present environmental changes. The effects of high temperatures on these organisms are being studied using stress resistance indicators, such as thermal shock proteins and the production of chemical defences (Lejeusne et al. 2010).

3.3.2. Predicted trends

Mass mortality events have occurred before in the northwest Mediterranean Sea. In September 1983, a mass mortality event affected the red coral populations up to 20 m depth in the Ligurian Sea (Harmelin 1984). Since then, other mortality events, mainly affecting cnidarians and sponges, have been ob-

Table 2. List of documented mass mortality events of invertebrates in the northwestern Mediterranean Sea. Extension: order of magnitude of affected coastline

Year	Location	Extension (km)	Scale	Depth range (m)	Taxon	Species	Reference
1983	La Ciotat (Ligurian Sea)	10 ⁰	Local	0 to 20	Cnidaria	<i>Corallium rubrum</i> <i>Eunicella singularis</i>	Harmelin (1984)
1987	Massala Lagoon (northwestern Sicily) Portofino (eastern Ligurian Sea)	10 ⁰ –10 ¹	Local	0 to 18	Porifera	<i>Spongia officinalis</i> <i>Anchinoe paupertas</i> <i>Ircinia variabilis</i>	Gaino & Pronzato (1989) Gaino et al. (1992)
1992	Medes Islands (northwestern Mediterranean)	10 ⁰	Local	0 to 13.5	Cnidaria	<i>Paramuricea clavata</i>	Coma & Zabala (1992)
1993	Sicily (southern Italy)	10 ⁰	Local	0 to 39	Cnidaria	<i>Paramuricea clavata</i>	Mistri & Ceccherelli (1996)
1994	Portofino Promontorio (Ligurian Sea)	10 ⁰	Local	0 to 35	Cnidaria	<i>Paramuricea clavata</i>	Bavestrello et al. (1994)
1994–1996	Porto Cesareo (South Adriatic Sea)	10 ⁰	Local	0 to 1	Porifera	<i>Ircinia spinosula</i> <i>Ircinia</i> sp.	Corriero et al. (1996)
1997–1999	Gulf of La Spezia (Ligurian Sea)	10 ¹	Local		Cnidaria	<i>Cladocora caespitosa</i> <i>Balanophyllia europaea</i>	Rodolfo Metalpa et al. (2000) Rodolfo-Metalpa et al. (2005)
1999	Coast of Provence and Ligurian Sea	10 ²	Regional	0 to 45	Cnidaria	7 species	Cerrano et al. (2000)
1999	Coast of Provence and Ligurian Sea	10 ²	Regional	0 to 45	Porifera Bryozoa Bivalvia Asciadiacea	12 species 4 species 2 species 3 species	Perez et al. (2000)
1999	Provence region (northwestern Mediterranean)			13 to 26	Cnidaria	<i>Corallium rubrum</i>	Garrabou et al. (2001)
1999	Balearic Islands (northwestern Mediterranean)			0 to 40	Cnidaria	<i>Eunicella singularis</i>	Coma et al. (2006)
2002	Ischia and Procida Islands (Tyrrhenean Sea)	10 ¹	Local		Cnidaria	<i>Paramuricea clavata</i> <i>Eunicella singularis</i>	Gambi et al. (2006)
2003	Gulf of Genova, Provence coast, Corsica–Sardinia, Gulf of Naples, Balearic Islands, Catalan coast	10 ³	Regional	0 to 40	Cnidaria Porifera Bryozoa Bivalvia	9 species 9 species 2 species 5 species	Garrabou et al. (2009)
2005	Columbretes Islands	10 ⁰	Local	0 to 16	Mollusca	<i>Spondylus gaeropus</i> <i>Barbatia barbata</i> <i>Arca noe</i>	Kersting et al. (2006)
2005	Phlaegrean Island (Tyrrhenean Sea)	10 ¹	Local		Cnidaria	<i>Eunicella cavolinii</i> <i>Eunicella singularis</i> <i>Paramuricea clavata</i>	Cigliano & Gambi (2007)
2007	Cabo de Palos–Cabrera Island (northwestern Mediterranean)	10 ⁰ –10 ¹	Local	0 to 45	Cnidaria	<i>Eunicella singularis</i> <i>Paramuricea clavata</i>	Coma et al. (2007)
2008–2009	Cabrera Island, Scandola National Park, Chafarinas Islands (northwestern Mediterranean)	10 ²	Regional	0 to 15	Porifera	<i>Ircinia fasciculata</i> <i>Sarcotragus spinosulum</i>	Maldonado et al. (2010) Cebrian et al. (2011)

served in the western basin (Table 2). A common characteristic of the events that occurred until 1999 was their localized distribution, in which damage affected tens of metres or kilometres. The 1999 episode was the first large regional event recorded (affecting hundreds of kilometres). The two extreme regional scale events (1999 and 2003) occurred concurrently with extreme events of stratification (Coma

et al. 2009). The current warming pattern and the observation that there is a relationship between the maximum temperature in summer and the lengthening of the stratification period (Coma et al. 2009) suggest that there will be an increased probability of long, hot summers in the northwest Mediterranean Sea and, therefore, in mass mortality events similar to those described above. This is consistent with the

pattern of increasing length of coastline affected by mass mortality events (Fig. 9). At present, the exposure to temperatures causing physiological stress under summer low-food conditions appears to be the main cause of major mass mortality events. However, the present warming trend forecast indicates a near future scenario that could increase current late summer metabolic stress, causing an increased production of heat shock proteins and a decrease in the production of chemical defences (Agell et al. 2001, Thomas et al. 2007). These circumstances would make organisms more susceptible to opportunistic, residential and pathogenic microorganisms, with an expected increase in virulence (Coma et al. 2009, Lejeusne et al. 2010, Vezzulli et al. 2010). Under this scenario, the exposure of organisms to lethal temperatures and susceptibility to opportunistic and pathogenic microorganisms may become more frequent. Regional hydrographic conditions are contributing to the explanation of the variability in the impact of mass mortality events in the Mediterranean Sea and to helping understand why the Catalan coast has, so far, been less affected than other northwestern Mediterranean areas (Garrabou et al. 2009, Bensoussan et al. 2010). The causal relationship between global warming and mass mortality events, reinforced by the observed increasing trend in the frequency and intensity of these events (Table 2, Fig. 9), suggests that there will be huge changes in the composition of the Mediterranean coralligenous community situated above the summer level of the thermocline. Increased frequency of mass mortality events suggests that the community may show a tendency to shift its upper distribution limit to a deeper level.

The effects of extreme events of warming and stratification on the coralligenous community are

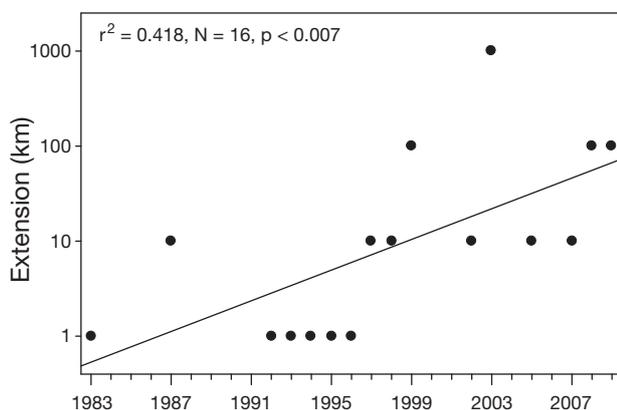


Fig. 9. Extension of the northwestern Mediterranean coastline affected by the documented mass mortality events. Note the y-axis is in log scale

among the clearest observations of biological effects associated with climate change (Coma et al. 2009). In this sense, the coralligenous community is one of the best indicators of climate change in the Catalan Sea and, in general, the northwestern region of the Mediterranean Sea (Ros 2009). Thus, given the evidence of limited dispersal of the main building species (Blanquer & Uriz 2010, Ledoux et al. 2010, Mokhtar-Jamaï et al. 2011), there is also an urgent need to act locally or regionally against the other relevant human disturbances, such as trawl fishing and waste water pollution (see Section 4), that reinforce climate change effects, if we are to avoid local extinction processes.

3.4. Fish populations

The ichthyofauna channels a significant part of the energy fixed by primary production, structures the biological community (playing a role at several trophic levels) and contributes to biodiversity (Worm et al. 2006). Climate change has both direct and indirect effects on fish populations. Direct effects act on their physiology and behaviour and indirect effects alter the productivity, structure and composition of the marine ecosystems on which fish depend for food (Brander 2010). Temperature is the most important abiotic variable governing growth, reproduction and survival of fishes (Magnuson et al. 1979, Stephens et al. 1988) and it determines species distribution, since different species have different fundamental thermal niches (Magnuson et al. 1979). The western Mediterranean region is characterised by a well defined seasonality, with relatively cold winters in the north and long hot periods in the south that are almost like those of subtropical regions. This latitudinal gradient marks the distribution of the species and their exploitation: the more thermophilic species are found along the coasts of North Africa and the southeastern Iberian Peninsula, while to the north, on the Catalan Sea coast and the Ligurian Sea, the species present are typical of colder waters. The most recent climate change is changing the 'traditional' geographic distribution patterns of fishes.

However, it is difficult to distinguish changes associated with climate variability from those related to other anthropogenic factors. Climate change is an additional pressure on top of many already experienced by fish stocks, such as fishing, loss of habitat, pollution and disturbance from introduced species (Brander 2010). This mix of pressures and forcings over fish populations, common to the entire planet

(Pauly et al. 1998), is also affecting the Mediterranean and the Catalan seas.

In addition, these climate- and human-induced changes in fish populations will have an effect on top predators like seabirds or cetaceans, whose distribution, abundance and migration largely depend on prey availability. An example of both direct and indirect effects of climate change on seabirds is the northward expansion of the endangered Balearic shearwater *Puffinus mauretanicus*. Their expansion into northeast Atlantic waters was attributed to a direct effect of warmer temperatures and an indirect effect through the influence of temperature on the distribution and composition of zooplankton, which nourish their fish prey (Wynn et al. 2007, Luczak et al. 2011). Recently, Gambaiani et al. (2009) highlighted the potential effects of climate change, in particular sea warming and the reduction of prey resources, on Mediterranean cetaceans such as common dolphins *Delphinus delphis*, bottlenose dolphins *Tursiops truncatus* or striped dolphins *Stenella coeruleoalba*.

3.4.1. Evidence of change

There is evidence that Mediterranean biodiversity patterns are changing and that these changes could be related to the increasing seawater temperature. Fish and benthic species from the warm waters of the southernmost parts of the Mediterranean are extending their distribution range to the north (e.g. Francour et al. 1994, Astraldi et al. 1995, Riera et al. 1995, Bianchi & Morri 2000, CIESM 2008a). More than 30 Mediterranean warmwater indigenous fish species have now been recorded north of their original geographical distribution. Similar poleward extensions have also been recorded outside the Mediterranean Sea (CIESM 2008a). Conversely, since the 1980s the abundance of some boreal species has dramatically decreased (Quignard & Raibault 1993, CIESM 2008a).

As an example, the ornate wrasse *Thalassoma pavo*, a warmwater species that lives in rocky habitats, is now commonly found on the Catalan Sea coast and the Gulf of Lion, while a few decades ago it was only found abundantly in more southern areas. The same is also the case for the pearly razorfish *Xyrichtys novacula*, the bluefish *Pomatomus saltatrix*, the bastard grunt *Pomadasyus incisus* and the dusky grouper *Epinephelus marginatus* (Francour et al. 1994). In the case of this last representative species, sea warming seems to favour their reproduction in the Catalan Sea (Zabala et al. 1997). Nevertheless,

other factors such as the increase in density of populations, due to establishment of marine protected areas in the last 20 yr, and recent modification of the sex ratio of populations, could have improved their reproductive success (Bodilis et al. 2003). The warming of the Mediterranean waters could also modify species' migration. Bluefin tuna *Thunnus thynnus* and the amberjack *Seriola dumerili*, for example, have lengthened their stay in northern and central Mediterranean waters before migrating towards their winter territories (Bombace 2001).

Recently, an increasing abundance and northward expansion of the round sardinella *Sardinella aurita* have been reported in the Catalan Sea (Sabatés et al. 2006). This species is a thermophilic, small, pelagic fish particularly abundant in the warm waters of the eastern as well as in the southwestern Mediterranean basin. A positive relationship was established between round sardinella catches and temperature anomalies in the western Mediterranean. A gradual increase in species abundance was also observed from south to north, with a certain time lag going northwards, associated with the increase in seawater temperature. Furthermore, successful reproduction of this species on the northern Catalan coast was reported close to the edge of its distribution range, confirming its establishment in the new distribution areas (Sabatés et al. 2009). Concurrently, sprat *Sprattus sprattus*, a coldwater species and very common on the Catalan Sea coast in the 1950s (Vives & Suau 1956) has practically disappeared from commercial landings in the last 25 yr (Catalan Government unpubl. fishing statistics).

Long-term fluctuations in abundance of small pelagic fishes in relation to climate variability and ocean regime shifts have been described in different regions around the world (e.g. Lluch-Belda et al. 1989, Kawasaki 1992). Small pelagic fishes have a short life span and feed on a short, plankton-based food chain, and their recruitment is controlled to a large extent by egg and larval survival that, in turn, is dependent on the prevalence of suitable oceanographic and climatic conditions. In the Catalan Sea coast, the sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus* are the most abundant small pelagic fishes. Fluctuations in abundance of these 2 species has been linked to local environmental conditions such as runoff from the Ebre and Rhône rivers, wind mixing, sea surface temperature and surface chl *a* during the previous spawning period (Lloret et al. 2001, 2004, Palomera et al. 2007, Martín et al. 2008). This may be explained by the increase of planktonic productivity as a result of river inputs, and

vertical mixing due to wind and low temperature, favouring spawning, feeding and survival of larvae. Recently, Martín et al. (2011) indicated that the WeMO regional index could provide an accurate representation of the environmental conditions affecting small pelagic fish production in the Catalan Sea. In this area, the abundance of these 2 species has fluctuated in synchrony over the last 30 yr. Positive WeMO phases, that is, low sea surface temperature, increased river flow and strong wind mixing, are favourable for the overall biological productivity in the Catalan Sea. In turn, this set of environmental factors would enhance survival and growth of sardines and anchovies during their life cycle, thereby increasing their recruitment (Martín et al. 2011).

The effect of climatic conditions on the dynamics of exploited populations has also been reported on demersal resources. Lloret et al. (2001) showed that Rhône River run-off was negatively affected by high NAO episodes. Although no relationship was established between NAO and fishery productivity of the northern Catalan coast, catches of different species were positively correlated with Rhône River outflow and the wind-mixing index during the previous spawning season. Thus, periods of low NAO index, generally coincident with high river run-off, tend to be more productive, favouring the recruitment and productivity of exploited stocks (Lloret et al. 2001). Similarly, in the Gulf of Lion, catches of the common sole *Solea solea* were also correlated with floods of the Rhône River (Salen-Picard et al. 2002) and with the abundance of polychaetes, their main prey. The increase in food after flooding events might favor the different stages of the sole's life cycle, enhancing its population size. In the Balearic Islands, Masutí et al. (2008) demonstrated that regional and global climate indices, such as NAO and MO, would influence the population dynamics of hake *Merluccius merluccius* and the deep-sea red shrimp *Aristeus antennatus*, favouring productivity and benefiting the recruitment of these species. On the Catalan coast, long-term variability in catches of the red shrimp and in the composition and diversity of deep sea communities have also been related to climatic oscillations (Maynou 2008, Cartes et al. 2009). Low or negative NAO phases, enhancing precipitation and river runoff, increased food input to deep benthos, which favour stocks of bottom-feeding species such as the red shrimp (Cartes et al. 2009). An enhancement of the recruitment process of this species and an increase of its total landings during the following years have also been associated with the

formation of dense and cold shelf waters and their subsequent downslope cascade inside submarine canyons, which is a climate-induced phenomenon (Company et al. 2008).

Feeding and survival of fish larvae and planktivorous fish may be affected by changes in the abundance and composition of food. Although no series of planktonic data are available for the Catalan Sea, Molinero et al. (2005, 2008b) and Fernández de Puellas & Molinero (2008) provided evidence of changes in the composition and phenology of the zooplankton (especially onset dates) associated with climate change for the Ligurian Sea and the Balearic Islands. According to those studies, the zooplankton is less abundant during high NAO phases (see Section 3.1.1). This would affect feeding and survival of fish larvae and subsequent recruitment. A paradigmatic case in this sense is Atlantic cod *Gadus morhua* in the North Sea. Declines in cod recruitment have been related to changes in the plankton ecosystem, due to rising temperatures since the mid-1980s, in a way that reduced the survival of larval cod (Beaugrand et al. 2003).

The relationship between recruitment of Mediterranean species and local (temperature, river discharges, wind conditions) and global (NAO, WeMO, MO) environmental conditions indicates the trophodynamic relationship between climate variability and fishery yields and illustrates how climatic forcing could influence the dynamics of ecosystem functioning at short- and long-term scales.

3.4.2. Predicted trends

The gradual warming predicted for the Mediterranean Sea, the intense fishing activity and the loss and degradation of habitat involve changes in the specific composition and abundance of fish communities. The progressive establishment on the northern Catalan Sea of species from more southern latitudes also seems to be irreversible; what needs to be studied is how these fish assemblage modifications might affect ecosystem function. It is uncertain what will happen to coldwater species living in the northern and colder areas of the western Mediterranean basin. Because they cannot move farther north, they may dramatically decrease in number or even be at risk of extinction (CIESM 2008a, Ben Rais Lasram et al. 2010). Moreover, evidence shows that Lessepsian fish species from the Red Sea have succeeded in invading the western basin of the Mediterranean Sea (e.g. Azzurro & Andaloro 2004, Dulčić & Pallaoro

2004, Daniel et al. 2009) because of global warming (Raitsos et al. 2010). Consequently, the spatial overlap between endemic and exotic fish species may lead to a reduction in the abundance and, in the future, a gradual replacement of endemic by exotic species (Ben Rais Lasram & Mouillot 2009). As those authors pointed out, this is a key issue in the conservation of biodiversity. In addition, temperature may also affect sex ratios in fishes, a key demographic variable crucial for population viability (Ospina-Álvarez & Piferrer 2008). Although it is still unclear to what extent a temperature increase may determine sex ratios in Mediterranean fishes, this effect will probably be more evident in the populations located on the geographic distribution limit of the species (Sabatés et al. 2006).

As indicated above, the predicted increase in water temperatures, lower wind stress and precipitation and the consequently higher stratification have also driven changes in the composition and phenology of planktonic communities (Molinero et al. 2005, 2008b) and the population size of gelatinous carnivores (Molinero et al. 2008a). These shifts may involve changes in trophic interactions of pelagic communities (Rossi et al. 2006) affecting the survival and growth of larvae and planktivorous fishes through effects on their prey, competitors and predators (Stige et al. 2010). Jellyfish outbreaks, for example, may significantly increase predation on fish larvae and competition with planktivorous fishes (Purcell & Arai 2001, Sabatés et al. 2010).

The exploited state of Mediterranean fishes can impair their resilience to climate change perturbations. Recent studies have shown how fishing can change the demographic structure of commercially targeted species and, therefore, the ability of populations to cope with a changing environment (Hidalgo et al. 2011). In the Mediterranean Sea, a large proportion of catches consists of young individuals (Leonart & Maynou 2003) and exploitation is highly dependent on recruitment, making such populations more sensitive to climate variability. Thus, it is evident that effects of climate change cannot be estimated without incorporating other human stressors. Marine ecosystems constitute 'social-ecological systems', including natural and human components, which are highly interconnected and interactive (Perry et al. 2010). In this context, it is important to develop integrated observational and modelling systems to quickly recognise changes, including those occurring due to human activity, to provide meaningful and realistic projections of climate change effects on natural resources (Barange et al. 2010).

4. ADDITIONAL ANTHROPOGENIC FACTORS AND POTENTIAL SYNERGIES

Climate change is only one of the anthropogenic stressors that are negatively affecting marine organisms and ecosystems. Additional human-related pressures include habitat destruction, overfishing, pollution and introduction of exotic species, to name a few. In addition to global warming, the increase in atmospheric CO₂ and its subsequent effect on ocean chemistry, have potentially negative consequences for many calcifying marine organisms (Fabry et al. 2008), including coccolithophores, which are important producers of calcium carbonate in the Mediterranean Sea. This change in seawater pH also affects the speciation, stoichiometry and the availability of essential nutrients (Hutchins et al. 2009 and references therein, Beman et al. 2011) and, therefore, could have an effect on primary productivity. More acidic conditions are expected to decrease the ammonia concentration at the expense of an increase in ammonium ions (Beman et al. 2011) and slightly reduce phosphate ion concentration (Hutchins et al. 2009). In the Mediterranean, which is generally limited by phosphorous, these changes could accentuate its oligotrophic character and lead to corresponding changes in plankton composition.

All these processes and variables have the potential to interact amongst themselves in different ways, including additive, synergistic or antagonistic interactions. Acidification and warming can act synergistically in worsening the calcification of corals and crustose coralline algae not only in tropical species (Reynaud et al. 2003, Anthony et al. 2008) but also in Mediterranean species (Martin & Gattuso 2009). Similar to what will probably occur in tropical coral reefs (Anthony et al. 2011), this combination of factors will contribute to reducing the resilience of coralligenous structures, potentially compromising the biodiversity that they contain. Currently, the coralligenous community is especially affected by trawl fishing (causing physical damage and increasing turbidity and sedimentation; Ballesteros 2008) and by introduced algae species (decreasing light availability to encrusting algae, increasing sedimentation, inhibiting recruitment and allowing overgrowth of some species; Ballesteros 2008, Klein & Verlaque 2008, 2009, Cebrian & Ballesteros 2009). Simulation studies have shown that mass mortality events driven by climate change dramatically reduce the viability of long-lived and low-turnover structural species of the community when combined with the effects of these additional anthropogenic impacts (Linares et al. 2010).

The growth, reproduction and formation of jellyfish swarms depend on a set of factors other than those that are strictly climatic. Jellyfish populations benefit from overfishing of commercially valuable fish that feed on the same prey as jellyfish, and overfishing of large carnivorous fish, along with turtles and seabirds, which are natural predators of jellyfish (Purcell et al. 2007). The proliferation of coastal species is also related to the settlement of polyps on artificial structures (Fuentes et al. 2010). This process benefits resident taxa such as *Aurelia* species, arguably the most widespread blooming jellyfish, and invasive species, such as the cubomedusa *Carybdea marsupialis* (Bordehore et al. 2011) whose invasion of the Mediterranean Sea is particularly concerning. Fishing is an important driver of structural and functional changes in the ecosystem (Coll et al. 2008) and also alters the demographic structure of fish populations, thereby modifying their ability to respond to climate variability and change (Planque et al. 2010, Hidalgo et al. 2011). Additional anthropogenic pressures are found in water management on land, which affects river discharges (Lloret et al. 2001) and habitat loss and degradation of waters and substrate necessary for fish spawning, feeding and growth (García-Rubies & Macpherson 1995, de Juan & Leonart 2010). Disentangling the combined effects of climate change and anthropogenic pressures on fish population dynamics is also of central importance for the understanding of ecosystem functioning, and thus for the management of exploited resources.

5. MANAGEMENT, MONITORING AND RESEARCH NEEDS

The most probable directions that changes in the ecosystems of the Catalan Sea will take encompass: (1) the 'meridionalisation' of the biota, which favours the most thermophilic native species and the arrival of foreign species; (2) the reduction of the biodiversity at higher trophic levels; (3) the disappearance of the most fragile and long-lived species with a low turnover, and a reduction in the 3-dimensional biogenic structure; (4) the loss of the capacity to recuperate; (5) the dominance of bottom-up controls in trophic webs in relation to top-down controls; (6) a reduction in the exported production to the sediments or to the trophic levels exploited by humans (Bianchi 2007, CIESM 2008a, Lejeune et al. 2010).

Environmental assessment and management for mitigating the effects of climate change on marine ecosystems is often based on the idea that the effects

are limited in time and the system will be able to recuperate quickly when the environmental pressure stops. Many initiatives aimed at making exploitation of the marine environment sustainable are based on this premise. Unfortunately, it is necessary to highlight the limited success of the tools currently used for managing the exploitation of marine resources. The progressive collapse of the fisheries around the world, for example, questions the supposed reversibility of human impacts in the short and medium term (Pauly & Watson 2005). In the case of climate change, the supposition of reversibility has been questioned from the beginning, due to the global character of climate change, its inertia (even if the atmospheric composition were held fixed at present values, the climate would continue to change, due to thermal inertia of the sea, Wigley 2005) and the non-linearity of its effects. Of special concern is that when a threshold is crossed, positive and negative feedbacks could shift ecosystems to a permanent alternative state that no longer functions in the same way as it did in the past (Lenton et al. 2008, Rockström et al. 2009).

Present evidence indicates that global warming is affecting the climate and hydrology of the western Mediterranean Sea and will continue to do so, leading to substantial changes in the composition and dynamics of marine ecosystems. Therefore, in addition to the work necessary for mitigating climate change and adapting to it, we need to take the following action:

(1) Reduce the effect of those disturbing factors we are more able to control (overfishing, destruction of habitats, pollution) and that may act synergistically with climate change to the detriment of marine ecosystems. Some studies aimed at determining the effects associated with climate change, such as the loss of biomass of benthic communities or the expansion of the range of distribution of warmwater species, indicate that the effects of climate change would be attenuated if we were able to reduce the effect of other disturbing factors (Ruiz et al. 2000, Linares et al. 2010). This would give us time to develop a more global action against climate change. However, to distinguish between the effects of climate change and those from other kinds of impacts, it is fundamental to have protected areas that are not affected by other anthropogenic factors that can act as baselines or 'controls'.

(2) Monitor the main physical, chemical and biological variables that are indicators of climate and environmental changes and the speed at which they are occurring. This monitoring should be carried out

systematically along the coast, but especially in protected areas where, because of management practices and the reduction of other impacting factors, we can discern and assess the effects of climate change. Time series studies, like the one from L'Estartit station and others that are currently underway, are fundamental for the understanding of climate change. The maintenance of these stations, as well as the establishment of new observatories—which could take advantage of initiatives to develop automatic measuring systems in buoys and fixed anchorages—is imperative. The data collected in time series can be used to detect and quantify the effects of climate change, and are vitally important for developing, testing and validating the climate and oceanographic models with which the climate predictions are made.

(3) Investigate the mechanisms and processes through which climate change acts on marine populations. Our capacity to predict the effects of climate change on the ecosystem depend on our degree of understanding of the mechanisms involved. This means that it is necessary to develop imaginative approaches to laboratory experimentation, environmental observation and modelling.

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Appendix 1. Climate change effects

Table A1. Summary of the effects of climate change on marine organisms

Organisms	Documented effects	Likely related cause or causes	Source
Planktonic primary producers and heterotrophs			
Phytoplankton			
Coastal assemblages	Decrease in overall biomass	Reduced eutrophication in the last decade	Mozeti et al. (2010), Ninčević Gladan et al. (2010)
Open sea assemblages in strongly stratified waters	Decrease in overall biomass	Longer lasting and stronger water column stratification	Goffart et al. (2002)
Open sea assemblages in strongly mixed waters	Increase in overall biomass, shift to smaller taxa	Earlier water column stratification	Marty et al. (2002)
Zooplankton			
Copepods	Changes in local species composition	NAO	Molinero et al. (2005)
	Substitution of copepods by gelatinous zooplankton	High NAO	Molinero et al. (2008b)
Bacterioplankton	Limited and inconclusive data		Duarte et al. (1999)
Jellyfish on the coast			
Cnidaria			
<i>Pelagia noctiluca</i> <i>Rhizostoma pulmo</i> <i>Physalia physalis</i> <i>Cotylorhiza tuberculata</i> <i>Aurelia aurita</i> <i>Veella veella</i> <i>Olindias phosphorica</i> <i>Aequorea forskalea</i> <i>Phyllorhiza pumctata</i> <i>Chrysaora hysoscella</i> <i>Porpita porpita</i> <i>Carybdea marsupials</i> Ctenophora <i>Mnemiopsis leiyi</i>	Increase in the frequency and number of swarms	Seawater temperature increase, overfishing, human recreation activities	Gili et al. (2010)
Coralligenous community			
Cnidaria			
<i>Paramuricea clavata</i>	Decrease in gonadal output of colonies	Extent of partial mortality, temperature and stratification increase	Linares et al. (2008b)
<i>Paramuricea clavata</i> <i>Eunicella cavolinii</i> <i>Eunicella sigularis</i> <i>Eunicella verrucosa</i> <i>Leptogorgia sarmentosa</i> <i>Corallium rubrum</i> <i>Cladocora caespitosa</i> <i>Balanophyllia italyca</i> <i>Oculina patagonica</i> <i>Parazoanthus axinellae</i>	Large increase in partial and total mortality	Seawater temperature, stratification increase	Cerrano et al. (2000), Perez et al. (2000), Linares et al. (2005), Coma et al. (2006, 2009), Garrabou et al. (2009)
Porifera			
<i>Spongia officinalis</i> <i>Ircinia dendroides</i> <i>Ircinia variabilis</i> <i>Ircinia oros</i> <i>Agelas oroides</i> <i>Crambe crambe</i> <i>Cacospongia</i> spp. <i>Hippospongia communis</i> <i>Petrosia ficiformis</i> <i>Spongia agaricina</i> <i>Clathrina clathrus</i> <i>Aplysina cavernícolas</i> <i>Reniera fulva</i>	Large increase in partial and total mortality	Seawater temperature, stratification increase/disease	Gaino et al. (1992), Coma & Ribes (2003), Maldonado et al. (2010), Cebrian et al. (2011)

Organisms	Documented effects	Likely related cause or causes	Source
Bryozoa <i>Myriapora truncata</i> <i>Sertella</i> spp. <i>Adeonella calveti</i> <i>Turbicellepora aviculari</i> <i>Pentapora fascialis</i> Bivalvia <i>Spondylus gaederopus</i> <i>Lima</i> spp. <i>Arca</i> spp. <i>Ostrea edulis</i> <i>Lithophaga lithophaga</i> <i>Neopycnodonte cochlear</i>	Large increase in partial and total mortality	Thermal anomaly, latent water-borne agent	Perez et al. (2000), Garrabou et al. (2009)
Ascidiacea <i>Microcosmus</i> spp. <i>Halocynthia papillosa</i> <i>Pyura dura</i>	Large increase in total mortality	Climatic anomaly; infection by microorganisms	Perez et al. (2000)
Fish and fisheries Fishes <i>Thalassoma pavo</i> <i>Xyrichtys novacula</i> <i>Pomatomus saltatrix</i> <i>Pomadasys incisus</i> <i>Sardinella aurita</i> <i>Epinephelus marginatus</i>	Northward range extension	Seawater temperature increase	Francour et al. (1994), Sabatés et al. (2006)
<i>Sardinella aurita</i>	Enhancing reproduction and recruitment	Seawater temperature increase	Sabatés et al. (2006), (2009)
<i>Engraulis encrasicolus</i>	Low catches	River runoff decrease, sea water temperature increase, low WeMO	Lloret et al. (2004), Palomera et al. (2007), Martín et al. (2008), Martín et al. (2011)
<i>Sardina pilchardus</i>	Low catches	River runoff decrease, sea water temperature increase, wind mixing decrease/ low WeMO	Lloret et al. (2004), Palomera et al. (2007), Martín et al. (2011)
<i>Solea solea</i>	Low catches	River runoff decrease	Salen-Picard et al. (2002)
Crustaceans <i>Merluccius merluccius</i>	High recruitment	Low or negative NAO	Massutí et al. (2008)
<i>Aristeus antennatus</i>	High catches, high spawning stock and abundance	Positive and high NAO and MO	Maynou (2008), Massutí et al. (2008)
<i>Aristeus antennatus</i>	Variability in catches	Shelf water cascading events	Company et al. (2008)

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