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REVIEW

Potential impacts of climate change and greenhouse gas emissions on Mediterranean marine ecosystems and cetaceans

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The combustion of fossil fuels and the resultant impacts on climate may now represent one of the largest environmental threats. In the Mediterranean Sea, changes in bio-chemical and physical seawater properties resulting from global warming are likely to alter marine biodiversity and productivity, trigger trophic web mismatches and encourage diseases, toxic algal bloom and propagation of thermophilic species. This review highlights the current and potential threats of climate change to the Mediterranean marine ecosystems, including cetaceans, and stresses the emergent necessity for more integrated regulations and policies for the protection of marine biodiversity. For instance, in the Mediterranean Sea, the distribution and abundance of the small euphausid species Meganyctiphanes norvegica *is correlated with specific hydrobiological parameters including seawater temperature, salinity and current patterns. Situated at the northern limit of its ecological tolerance, this species, which constitutes the only known food supply of the fin whales* (Balaenoptera physalus) *in this region, might be affected by climate change-induced alteration of ocean circulation.*

Keywords: potential impacts, climate change, greenhouse gas emissions, Mediterranean, marine ecosystems, cetaceans

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INTRODUCTION

Until recently, scientists have hesitated to associate the global warming phenomenon with anthropogenic greenhouse gas emissions. However, a strong correlation has been demonstrated along with other supporting evidence and it is now generally accepted that greenhouse gas emissions are responsible for global warming (e.g. Tett *et al.*, 2000; Smith *et al.*, 2005; IPCC, 2007a). We know that our carbon dioxide emissions, which represent ~7 gigatons (Gt) of carbon per year (Bopp *et al.*, 2002), are responsible for disastrous ecological disorders. Each year, 2 Gt of carbon is absorbed by the oceans through physical and biological processes but, this 'carbon pump' could be saturated by 2020–2030 (Orr *et al.*, 2001). A significant reduction in the efficiency of the Southern Ocean sink of CO_2 has recently been observed (Le Quéré *et al.*, 2007). Studies indicate that climate/carbon cycle feedbacks could be responsible for an additional increase of the partial pressure of CO_2 in the atmosphere of 10% to 50% (Cox *et al.*, 2000). Working Group 1 of the Intergovernmental on Climate Change (IPCC) shows that, according to different scenarios, the average warming of the planet will be between 1.8 and 4°C by 2100 (IPCC, 2007b). Such an increase of temperature in a very short time period represents a real 'climatic shock' for which no solution has yet been considered by our society (Jancovici, 2005).

Positive feedback processes would tend to accelerate the rate of global warming (Woodwell & Mackenzie, 1995). The amount of methane sequestered as methane hydrates in the oceanic sediments of continental plates, as well as in permafrost regions, could be 3000 times larger than the amount of methane present in the atmosphere (Blunier, 2000). With an increase of water temperatures, methane hydrates could become unstable and release vast quantities of methane into the atmosphere. Given that methane is 20 times more efficient than carbon dioxide at trapping infrared radiation, this could have catastrophic climatic consequences. Such an event, known as a 'methane burp', occurred about 200 million years ago. By increasing the atmospheric temperature by 4 to 8 degrees, and reducing the amount of oxygen, this phenomenon may have been responsible for the extinction of 80% of the oceanic fauna at that time (Hesselbo *et al.*, 2000; Kennett *et al.*, 2000).

Atmospheric carbon dioxide is also known to be absorbed by the oceans, leading to ocean acidification. This process is already

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affecting surface waters (Royal Society, 2005) and future increases in atmospheric carbon dioxide via the combustion of fossil fuels are expected to profoundly affect ocean chemistry and marine life (Caldeira & Wickett, 2003; Feely *et al.*, 2004; Royal Society, 2005; Orr *et al.*, 2005; Bass *et al.*, 2006).

Global warming is already affecting marine ecosystems (CBD, 2003; Parmesan & Yohe, 2003). According to Thomas *et al.* (2004), climate change is today one of the most serious threats to biodiversity and 'on the basis of mid-range climate warming scenarios for 2050, 15–37% of species in our sample of regions and taxa will be "committed to extinction"'.

As a miniature ocean (0.82% of the world's ocean surface) with fast turnover time (40–50 years) the semi-enclosed Mediterranean, which accounts for 8% to 9% of global marine biodiversity and contains numerous endemic species (Bianchi & Morri, 2000), is likely to rapidly respond to external forcing like climate change (Béthoux & Gentili, 1996; Monaco, 1998; Béthoux *et al.*, 1999; Turley, 1999; Simmonds & Nunny, 2002; Giorgi, 2006).

The aim of this review is to illustrate the links existing between biodiversity and climate and demonstrate how anthropogenic greenhouse warming can affect the Mediterranean marine ecosystems including large predators such as cetaceans. It illustrates the impacts of global warming on abiotic and biotic systems in the Mediterranean Sea and stresses the necessity to consider climate change as a major issue.

DISCUSSION

Influence of climate change on Mediterranean abiotic parameters

By influencing climatic features (e.g. atmospheric temperature, precipitation budget and extreme meteorological events), global warming is likely to affect the chemical and physical properties of Mediterranean waters.

Present and future trends of Mediterranean climate and hydrology

At the beginning of the 20th Century, the temperature and salinity of the Western Mediterranean Deep Water (WMDW) was practically constant (Lacombe *et al.*, 1985; Béthoux *et al.*, 1990). Over the last few decades, numerous studies have indicated a correlation between climate patterns and changes in seawater properties, with general increases in both temperature and salinity over the entire Mediterranean (Lacombe *et al.*, 1985; Béthoux *et al.*, 1990; Leaman & Schott, 1991; Rohling & Bryden, 1992; Francour *et al.*, 1994; Sparnocchia *et al.*, 1994; Astraldi *et al.*, 1995; Graham, 1995; Béthoux & Gentili, 1996; Béthoux *et al.*, 1998, Krahmann & Schott, 1998; Duarte *et al.*, 1999; Danovaro *et al.*, 2001; Astraldi *et al.*, 2002; Fuda & Millot, 2002; Gertman & Hecht, 2002; Goffart *et al.*, 2002; Lascaratos *et al.*, 2002; Lopez-Jurado, 2002; Manca *et al.*, 2002; Prieur, 2002; Salat & Pascual, 2002; Vargas-Yanes *et al.*, 2002; Vilibic, 2002; Walther *et al.*, 2002; Rixen *et al.*, 2005; Li *et al.*, 2006; Millot *et al.*, 2006; Somot *et al.*, 2006). It is now assumed that the WMDW has become warmer and saltier in response to anthropogenic greenhouse effects and changes in the freshwater budget (Béthoux *et al.*, 1990; Rohling & Bryden, 1992; Graham, 1995; Béthoux *et al.*, 1998).

Furthermore, from 1900 to 2000, the Mediterranean experienced a 10% decrease in summer rainfall (IPCC, 2001a). These trends are expected to persist and intensify over time, and extreme meteorological events such as droughts (e.g. in the summers of 1995 and 2003) and flooding will become more frequent in the future (e.g. Parry, 2000; IPCC, 2001b; Li, 2003; EEA, 2004; Giannakopoulos *et al.*, 2005; Xoplaki *et al.*, 2005; Luterbacher *et al.*, 2007). By the 2020s, under high CO_2 scenarios, summer in southern Europe will be as hot as or hotter than the 2003 summer (Luterbacher *et al.*, 2004).

Font *et al.* (2007) have documented that the exceptional winter of 2005 affected the deep-water thermohaline properties of the north-western Mediterranean. Similarly, in the Aegean Sea, it is likely that changes in the freshwater budget could have modified seawater salinity and altered water-mass circulation (Roether *et al.*, 1996; Theocharis *et al.*, 1999). Climate variation—including extreme events—is not necessarily a result of directional climate change. However, climate change is likely to create more extreme meteorological events (e.g. storms and drought), and these can alter the biochemical and physical properties of seawater (Poumadère *et al.*, 2005; Olita *et al.*, 2007).

SEA LEVEL RISE

Ecologically and socio-economically rich coastal marine systems are under threat from anthropogenic global warming (IPCC, 2001a; Roessig *et al.*, 2004). Sea level rise resulting from climate change-related processes such as seawater thermal expansion or glacier melt will trigger coastal flooding (Paskoff, 2001). According to Tsimplis & Rixen (2002) from 1993 onwards, the warming of surface waters in the Eastern Mediterranean has caused sea level rise. In the last century, sea level has risen by 0.10 to 0.20 m around Europe (IPCC, 2001a) and an increase of sea level of 3.3 cm in 11 years (0.3 cm per year) was recorded at the oceanographic and meteorological station at l'Estartit in north-east Spain (Salat & Pascual, 2002). Between 1990 and 2100, the predicted trend for sea level rise is 2.2 to 4.4 times higher than the rate recorded in the 20th Century (IPCC, 2001a). Consequently, some Mediterranean coastal areas and wetlands, such as the Camargue, are threatened (Nicholls & Hoozemans, 1996; Pfeifle *et al.*, 2004).

ATMOSPHERIC CHANGE AND CLIMATE IMPACTS IN THE MEDITERRANEAN

Anthropogenic climate change tends to influence large atmospheric patterns like the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Timmermann *et al.*, 1999; Visbeck *et al.*, 2001; Würsig *et al.*, 2002; Cohen & Barlow, 2005). Global warming is likely to contribute to the positive phase of the NAO, which was responsible for warmer winters in Europe in the last 10–20 years (Hurrell, 1996; Visbeck *et al.*, 2001; Gillet *et al.*, 2003; Cohen & Barlow, 2005) and El Niño conditions may be more frequent with global warming (Timmermann *et al.*, 1999; Würsig *et al.*, 2002).

The Mediterranean climate is influenced by large-scale atmospheric circulation systems including the inter-decadal NAO and ENSO (Hurrell, 1995; Raicich *et al.*, 2001; Mariotti *et al.*, 2002; Lionello & Sanna, 2005). Changes in Mediterranean seawater temperature and salinity have been associated with the NAO (e.g. Béthoux & Gentili, 1999; Béthoux *et al.*, 1999; Tsimplis *et al.*, 2006). In fact, the

NAO influences Mediterranean precipitation and river discharges (nutrient inputs), which tend to be lower during positive NAO episodes (Lloret *et al*., 2001; Struglia *et al*., 2004; Xoplaki *et al*., 2004, 2006). According to Tsimplis & Josey (2001), NAO is also influencing sea level change in the Mediterranean Sea. Mariotti *et al*. (2002) have also identified a link between ENSO and Mediterranean autumn rainfall anomalies. The relationship between NAO, ENSO and climate change is an important issue and requires further study.

Climate change impacts on Mediterranean marine biodiversity and ecosystems

Evidence has demonstrated that climate variation and changes in the properties of ecological systems are strongly correlated (e.g. Orr *et al*., 1992; Astraldi *et al*., 1995; Bombace, 2001; Hannah *et al*., 2002; Walther *et al*., 2002; Duffy, 2003; Root *et al*., 2003; Roessig *et al*., 2004) and that global warming is already affecting numerous marine species throughout the world (Table 1). In the Mediterranean, it is now acknowledged that climate change-induced temperature variations have altered biological patterns and biodiversity (e.g. Francour *et al*., 1994; Turley, 1999; Bianchi & Morri, 2000).

Table 1. Examples of species affected by climate change induced-factors around the world (Mediterranean Sea excluded).

Areas	Examples of affected species
North-east Atlantic	• Marine flora: Ducrotoy (1999) • Plankton: Southward *et al*. (1995); Fromentin & Planque (1996); Nehring (1998); Planque & Taylor (1998); Heath *et al*. (1999); Edwards *et al*. (2001); Beare *et al*. (2002); Beaugrand *et al*. (2002); Edwards *et al*. (2002); Sims & Reid (2002); Beaugrand (2003); Beaugrand & Reid (2003); Edwards & Beaugrand (2007); Greve (2007); Pitois & Fox (2007); Slagstad *et al*. (2007); Voss *et al*. (2007) • Intertidal and benthic organisms: Southward *et al*. (1995); Kroncke *et al*. (1998) • Fish: Scarnecchia (1984); Svendsen (1995); Alheit & Hagen (1997); Southward *et al*. (1988); Sims & Reid (2002); Beaugrand & Reid (2003); Beaugrand *et al*. (2003); Clark *et al*. (2003); Genner *et al*. (2004); Sims *et al*. (2004); Brander (2005); Cotton *et al*. (2005); Perry *et al*. (2005); Rose (2005); Sissener & Bjorndal (2005); Pörtner & Knust (2007); Stenevik & Sundby (2007); Voss *et al*. (2007) • Cephalopods: Sims *et al*. (2001)
Tropical Atlantic	• Plankton: Piontkovski & Castellani (2007)
Antarctic Peninsula	• Plankton: Moline *et al*. (2004)
Bay of Biscay	• Fish: Poulard & Blanchard (2005)
North Pacific Ocean	• Plankton: Roemmich & McGowan (1995); Brodeur *et al*. (1999); Batten (2007)
Worldwide	• Coral reefs: Sebens (1994); Sheppard (1999); Spalding *et al*. (2003)

potential effects of climate change-induced environmental variations on mediterranean marine species

1. Climate impacts on marine fauna

The global warming-induced alteration of precipitation, temperature, CO_2 concentration and wind patterns will result in a cascade of changes in the physical (e.g. vertical stability of the water column, upwelling regimes, water mass formation and circulation, current patterns), chemical (e.g. seawater pH, salinity, nutrient ratios) and biological (e.g. species phenology, recruitment, physiology, distribution, abundance, diversity, productivity) properties of marine systems (Figure 1) (e.g. Bianchi, 1997; Walther *et al*., 2002). Temperature anomalies, even over a short period of time, can significantly affect Mediterranean ecosystems and biological diversity (Walther *et al*., 2002; Anadón *et al*., 2007). When a keystone species is affected, even by a slight change in climate, the composition and diversity of marine communities can be disrupted (Sanford, 1999). The structure, distribution and phenology of Mediterranean plankton communities, which are at the base of the food chain and which strongly depend on hydroclimatic factors and nutrient ratios, are experiencing change (Velsch, 1997; Turley, 1999; Licandro & Ibanez, 2000; Béthoux *et al*., 2002; Fernandez de Puelles *et al*., 2004; Mercado *et al*., 2005; Molinero *et al*., 2005a, b; Molinero *et al*., 2007; Voarino, 2006). For instance, high positive anomalies in water temperature during the 1980s resulted in jellyfish and a drop in abundance of copepods (Molinero *et al*., 2005a).

Climate has long been recognized as one of the most critical factors influencing Mediterranean resource variability (Garcia & Palomera, 1996). For instance, the most essential environmental mechanisms controlling the growth, abundance, distribution, composition, diversity and recruitment success of Mediterranean species, such as anchovy (*Engraulis encrasicolus*) or sardine (*Sardinella aurita* and *Sardina pilchardus*), include: regional temperature variations, riverine inputs and wind-induced mixing, which influence sea surface temperature and salinity; hydrographical features (e.g. oceanic fronts, water column stability, upwelling zones, sea state); and nutrient enrichment and planktonic production (e.g. Cury & Roy, 1989; Sabates & Gili, 1991; Garcia & Palomera, 1996; Regner, 1996; Agostini & Bakun, 2002; Lafuente *et al*., 2002; LLoret *et al*., 2004; Lafuente *et al*., 2005; Basilone *et al*., 2006; Sabates *et al*., 2006).

The Mediterranean Sea is considered oligotrophic because of its low nutrient input from rivers and the nutrient depleted Atlantic water inflow through the Strait of Gibraltar (e.g. Estrada, 1996; Turley, 1999; Zenetos *et al*., 2002). Winter vertical mixing, coastal upwelling and river runoff are the mechanisms of nutrient input into the euphotic zone, on which marine productivity is dependent. Ocean physical processes such as upwelling phenomena have a major influence on the distribution of primary production, through ascending movements of nutrient-rich deep water into the euphotic zone. Therefore, by altering oceanic features, climate change may affect nutrient availability.

Increasing temperatures are likely to trigger stronger thermal stratification and deepen the thermocline, which could prevent or modify the mixing of water-masses, and cold and nutrient-rich deep waters upwelling (Roemmich & McGowan, 1995). Some areas like the southern Adriatic Sea, where local winter climatic conditions (e.g. winter heat

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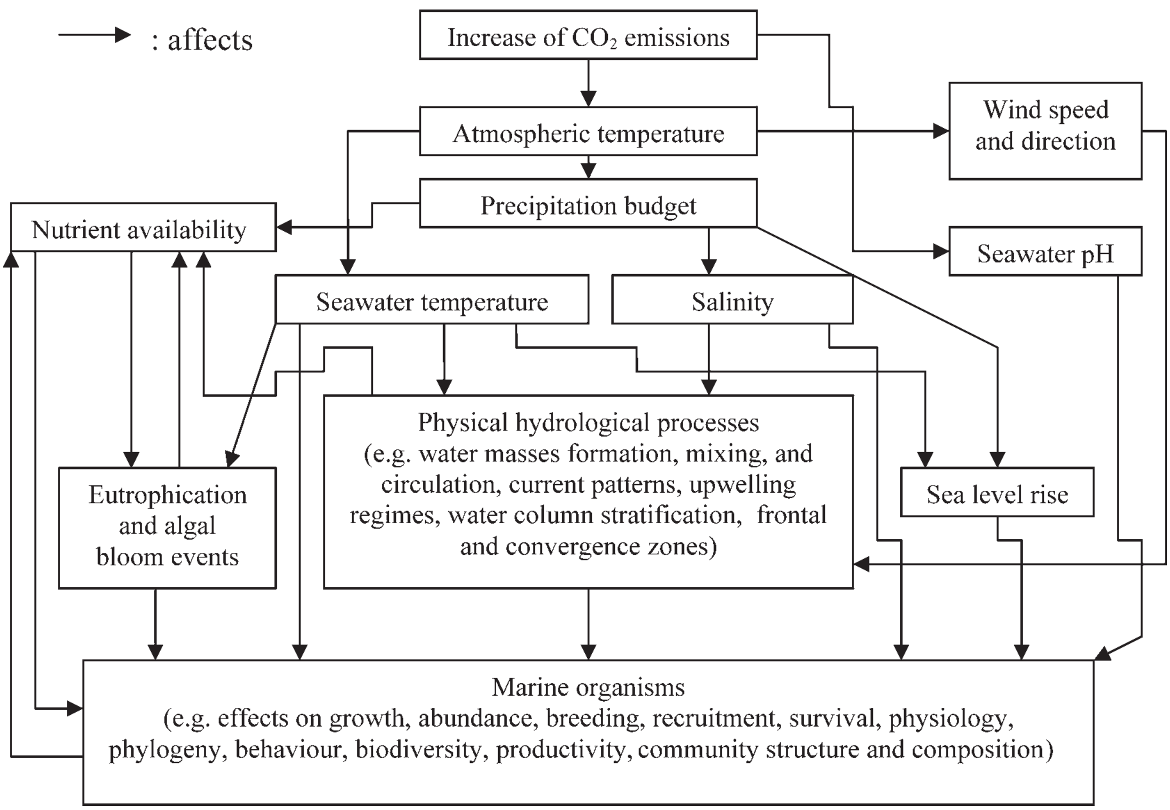

Fig. 1. Main greenhouse gases-related factors influencing marine organisms.

losses and precipitation) strongly influence nutrient availability and plankton production (Gacic, 2002), may be especially vulnerable to climate change.

Extreme meteorological events (e.g. storms and flooding episodes) and sea level rise will release abundant terrestrial suspended solids and pollutants into the marine environment, which may negatively affect coastal biocenoses. Fragile biotopes of the endemic *Posidonia oceanica* have been shown to be vulnerable to physical and chemical damage from meteorological events such as these (Orr *et al.*, 1992; Bombace, 2001). As these sea grass meadows represent a spawning and nursery habitat for numerous species and play a major ecological role, their disappearance would to expected to have significant consequences for coastal ecosystems (Francour, 1997).

By influencing the north-western Mediterranean climate variability (Pozo-Vasquez *et al.*, 2001; Gasparini & Astraldi, 2002; Rixen *et al.*, 2005), the NAO affects the local species composition of planktonic copepods, such as the two dominant copepods of the north-west Meditarranean, *Centropages typicus* and *Temora stylifera* (Molinero *et al.*, 2005a, b).

The high positive NAO episode that caused positive temperature anomalies in the 1980s in the western Mediterranean Sea induced a jellyfish bloom and resulted in a significant diminishment of copepod abundance (Molinero *et al.*, 2005a). This event, which is likely to have been encouraged by global warming, led to high abundance of *Centropages typicus* at the expense of *Temora stylifera* (Molinero *et al.*, 2005b). Jellyfish, which feed on fish larvae, eggs and copepods, can strongly affect plankton communities (Mills, 1995). Changes in planktonic copepods, which affect the fluxes of matter and energy in the marine ecosystem, supply a biological pump of carbon into the deep ocean and strongly influence fish recruitment could alter the ecosystem functioning (Ohman & Hirche, 2001; Molinero *et al.*, 2005b).

Nutrient inputs from the Rhône and Ebre rivers, combined with strong wind mixing, make the north-western Mediterranean highly productive (Lloret *et al.*, 2001). As previously noted, climate change is expected to induce positive NAO episodes with less precipitation and runoff. Consequently, the recruitment of north-western Mediterranean fish, which strongly depend on riverine nutrient supply, may be negatively affected by climate change (Lloret *et al.*, 2001).

In certain areas some organisms survive under specific temperature conditions and cannot adapt themselves or move when the environmental conditions change (e.g. Kenney, 1990; MacGarvin & Simmonds, 1996; Hughes, 2000). Dispersal limitation can limit the response of marine animals such as benthic organisms that could sometimes be unable to successfully migrate toward more suitable environments (problems would include long distances or travelling against strong currents) (Hiscock *et al.*, 2004).

By affecting the physiology of marine organisms, global warming could impact the performance and survival of those organisms that live close to their thermal tolerance or situated at the northern or southern limit of their distribution (Laubier, 2001; Hochachka & Somero, 2002; Somero, 2002; Poulard & Blanchard, 2005). Similarly, some larval and young benthic stages of some organisms are more sensitive to temperature than adults (Foster, 1971; Pechenik, 1989). According to Bella Galil in Cheviron (2007), deep-water organisms that live in constant temperatures (~13°C) and that are not used to seasonal temperature variation will be vulnerable to climate change.

2. Climate impacts on marine flora

Climate change is likely to affect phytoplankton composition by affecting nutrient concentrations and ratios. Over the last two decades, in the north-western Mediterranean, meteorological anomalies (e.g. warmer water, decreased salinity, longer periods of sunshine and lower wind stress) have affected water column stability and reduced nutrient replenishment into the euphotic zone (Goffart *et al.*, 2002). This event decreased silicon availability, which in turn triggered a reduction of diatom abundance and a shift toward non-siliceous species, such as flagellates and dinoflagellates (Turley, 1999; Béthoux *et al.*, 2002; Goffart *et al.*, 2002). By modifying the composition of phytoplankton communities, climate change could then seriously alter nutrient cycling and food web dynamics (Litchman *et al.*, 2006).

Warmer temperatures trigger changes in the timing of plankton blooms, resulting in a temporal mismatch between primary production and higher trophic levels of the food web (Edwards & Richardson, 2004; Hiscock *et al.*, 2004). In north-western European estuaries, for example, a long-term data set (1973–2001), showed an increase of spring temperatures of 0.07°C yr^{-1}, which resulted in the earlier spawning of a bivalve, *Macoma balthica*, but did not affect phytoplankton blooms, causing a divergence in timing between larval bivalve production and prey (Philippart *et al.*, 2003). In addition, rising seawater temperatures advance the onset of crustacean reproduction and enhance shrimp predation pressure on vulnerable juvenile spat that leads to low recruitment success of the spat (Philippart *et al.*, 2003).

MIGRATION OF SPECIES AND INCREASED NUMBER OF EXOTIC THERMOPHILIC SPECIES IN THE MEDITERRANEAN SEA

The presence of exotic species in the Mediterranean has resulted from the combination of environmental factors and human activities like the opening of the Suez Canal in 1869. Today, more than 500 alien species are recorded in the Mediterranean Sea and their geographical ranges are increasing, as is the rate of increase of new alien species being identified (Galil & Zenetos, 2002; Zenetos *et al.*, 2003; Harmelin-Vivien *et al.*, 2005; CIESM, 2005; Galil, 2007). Climate change, combined with the establishment of exotic species has led to the 'tropicalization' of the Mediterranean (Bianchi, 2007). The increase of alien species can cause endemic species to rapidly decline in abundance and be displaced (Galil & Zenetos, 2002; Zenetos *et al.*, 2002; Galil, 2007). Such phenomena can alter the infra-littoral communities and induce ecological impacts such as local population decline and extirpation, reduction of genetic diversity in native species, foodweb alterations, loss of habitat functions, processes and structure, increase in the risk of extinction and biotic homogenization (Ricciardi, 2004; Galil, 2007).

In the North Atlantic Ocean, the observed northward migration of species (250 km per decade), resulting from a minor increase in temperature, is likely to be linked to global warming (Parmesan & Yohe, 2003; EEA, 2004; Oviatt, 2004). Perry *et al.* (2005) have also demonstrated that, in the North Sea, recent increases in sea temperature have led to nearly two-thirds of fish species (exploited and non-exploited) shifting in mean latitude or depth or both over 25 years. For species with northerly or southerly range margins in the North Sea, half showed boundary shifts with warming, and all but one species shifted northward.

In the Mediterranean, over the past three decades, increasing water temperature has been observed in the Ligurian Sea (Béthoux *et al.*, 1990; Astraldi *et al.*, 1995), which is one of the coldest zones of the Mediterranean. This phenomenon encouraged warm-water species to shift their ranges northward and settle in the Ligurian waters where they were formerly rare or absent (Bianchi & Morri, 1993, 1994; Francour *et al.*, 1994; Astraldi *et al.*, 1995; Morri & Bianchi, 2001).

Consequently, warm-water species like the ornate wrasse (*Thalassoma pavo*) colonized and established large and stable populations in the north-western Mediterranean (Bianchi & Morri, 1994; Bombace, 2001; Vacchi *et al.*, 2001). Other thermophilic species like the grey triggerfish (*Balistes carolinensis*), Mediterranean parrotfish (*Sparisoma cretense*), round sardine (*Sardinella aurita*), bluefish (*Pomatomus saltatrix*), Senegalese sole (*Solea senegalensis*), dusky grouper (*Epinephelus marginatus*), bastard grunt (*Pomadasys incisus*), European barracuda (*Sphyraena sphyraena*), slackskin blaasop (*Sphoeroides cutaneus*), the coral *Astroides calycularis* and groupers of the genus *Epinephelus* have been frequently recorded amongst the 'cold biota' of the northern Mediterranean (Vacchi & Cau, 1986; Serena & Silvestri, 1996; Relini & Orsi Relini, 1997; Dulcic *et al.*, 1999; Louisy & Culioli, 1999; Dulcic & Grbec, 2000; Guidetti & Boero, 2001; Dulcic *et al.*, 2005, 2006; Athanassios & Antonopoulou, 2006).

The recent northward expansion of tropical groupers, like the white grouper (*Epinephelus aeneus*) and dusky grouper (*Epinephelus marginatus*), may result from the warming of Mediterranean waters (Francour *et al.*, 1994; Dulcic & Lipej, 1997; Zabala *et al.*, 1997). Since groupers are top carnivores and among the bigger coastal fish species, their successful colonization is likely to affect the ecology of endemic species and influence local fisheries (Glamuzina, 1999).

Similarly, in the Adriatic Sea, the presence of thermophilic species of fish and zooplankton, that were formerly uncommon or absent in this zone, has increased in the past 30 years (Dulcic & Grbec, 2000; Kamburska & Fonda-Umani, 2006). These observations have been correlated with seawater warming and salinity changes occurring since 1988 (Francour *et al.*, 1994; Russo *et al.*, 2002) and, thus, global warming is thought to be responsible for the observed faunal changes in this region (Dulcic *et al.*, 1999; Dulcic & Grbec, 2000; Parenti & Bressi, 2001).

The northward migration of warm water species will induce species competition for existing niches (IPCC, 2001a) and thermophilic species are likely to increase in abundance at the expense of cold-water species (Beaugrand *et al.*, 2002; Galil & Zenetos, 2002; Hiscock *et al.*, 2004). Marine bioinvasions, which are considered to be 'biological pollution' (Bouderesque & Verlaque, 2002; Elliot, 2003) have altered marine ecosystems (e.g. competition with indigenous species, food web shifts) and are considered as one of the most intense and damaging anthropogenic impacts (Harris & Tyrrell, 2001; Frank *et al.*, 2005; Galil *et al.*, 2007). The Mediterranean Sea is one of the most impacted seas of the world in terms of biological invasion (Galil, 2007) and climate change is likely to facilitate invasion of thermophilic alien species causing irreversible impacts on native populations (Carlton, 2000; Stachowicz *et al.*, 2002b; Gritti *et al.*, 2006; Galil *et al.*, 2007; Occhipinti-Ambrogi, 2007). According to Bella Galil (in Cheviron, 2007) alien species like the bivalve *Brachidontes pharaonis* or the jellyfish *Rhopilema nomadica*, both belonging to the 100 'worst invasives' species, could lead to the extinction of numerous native Mediterranean species. Photophilic subtidal macrophyte assemblages appear particularly vulnerable to invasions of exotic algal species such as *Caulerpa taxifolia* (Streftaris & Zenetos, 2006).

In addition to northward migration, bathymetric displacements occur among populations of invasive and endemic species (Galil & Zenetos, 2002). This is the case for the indigenous red mullet (*Mullus barbatus*) and hake (*Merluccius merluccius*) with both moving into deeper and cooler waters due to their respective warm-water competitors: the goldband goatfish (*Upeneus moluccensis*) and brushtooth lizardfish (*Saurida undosquamis*) (Oren, 1957). Similarly, in the north-western Mediterranean, the endemic spottail mantis shrimp (*Squilla mantis*) is usually observed in deeper waters (70–80 m) rather than the thermophilic Red Sea mantis shrimp (*Oratosquilla massavensis*) (10–25 m) (Galil & Zenetos, 2002).

The warming of the Mediterranean waters may modify species' migration periods causing changes in the trophic webs. For example, Bombace (2001), has documented that in the last few decades, the amberjack (*Seriola dumerilii*) and bluefin tuna (*Thunnnus thynnus*) appear to stay longer (until mid-winter instead of autumn) in the northern and central Mediterranean before migrating toward their winter territories.

Although there are presently no marine species extinctions that have been correlated with global warming, today, species such as the Mediterranean mysid *Hemimysis speluncola* are regarded as threatened (Chevaldonné & Lejeusne, 2003; Lejeusne, 2005; Lejeusne & Chevaldonné, 2005; Harley *et al.*, 2006). Furthermore, Chevaldonné & Lejeusne (2003) showed that the endemic cave-dwelling invertebrate *Hemimysis speluncola* which was previously abundant in the north-western Mediterranean, has been replaced by a warm-water species (*Hemimysis margalefi*).

Areas of high endemic biodiversity are likely to be less subject to non-indigenous species invasion (Kennedy *et al.*, 2002; Stachowicz *et al.*, 2002a; Duffy, 2003). Therefore, sparse and declining populations such as *Posidonia* meadows are more vulnerable to be overgrown and replaced by invasive macroalgae like *Caulerpa taxifolia* and *Caulerpa racemosa* (Meinesz *et al.*, 2001; Bouderesque & Verlaque, 2002; Peirano *et al.*, 2005). Climate change could be one of the factors responsible for the decline of *Posidonia* and for the expansion of *Caulerpa* (Komatsu *et al.*, 1997; Raniello *et al.*, 2004; Peirano *et al.*, 2005; Ruitton *et al.*, 2005).

Furthermore, some cold-water species like the small euphausid species *Meganyctiphanes norvegica*, which is situated at the northern limit of its ecological tolerance, would be more vulnerable to invasion. This is especially true for many taxa in the eastern Mediterranean, leaving this region more exposed to invasion (Galil & Zenetos, 2002).

LARGE MASS-MORTALITY EVENTS AND DECLINE IN SPECIES ABUNDANCE AND DIVERSITY ASSOCIATED WITH TEMPERATURE ANOMALIES

Temperature anomalies have led to several mass-mortality episodes in the Mediterranean Sea. In 1999, successive heat waves with consequent peaks in water temperature and a deepening of the thermocline caused a mass-mortality event of 28 invertebrate species in the north-western Mediterranean (Cerrano *et al.*, 2000; Perez *et al.*, 2000; Romano *et al.*, 2000; Laubier *et al.*, 2003). This event affected benthic organisms such as gorgonians, sponges, cnidarians, bivalves, ascidians, bryozoans, scleractinian corals and zoanthids (Cerrano *et al.*, 2000; Perez *et al.*, 2000; Romano *et al.*, 2000; Garrabou *et al.*, 2001). According to Occhipinti-Ambrogi (2007), niches resulting from mass mortality events become available for new invasive colonizers.

Variations of the nutrient load and seawater properties (e.g. temperature increase) can lead to coastal eutrophication and algal bloom (Degobbis *et al.*, 2000). This phenomenon particularly concerns the shallow northern Adriatic waters (UNEP, 1996; Degobbis *et al.*, 2000). By increasing seawater stratification, meteorological anomalies regularly cause bottom water anoxia and red tide events in this region, provoking mass mortality episodes of fish and benthic organisms (Degobbis *et al.*, 2000; Anadón *et al.*, 2007). Eutrophication events occurred frequently during the second half of the 20th Century (Degobbis *et al.*, 2000) and the intensity, frequency and geographical expansion of algal blooms became a growing concern since the 1970s in this area (Justic, 1987). According to Boero (1996), increases in jellyfish (*Pelagia noctiluca* and *Aurelia aurita*), salps (Thaliacea), harmful algal blooms and red tides were all promoted by abnormal meteorological and oceanographic changes occurring since 1988 in the Adriatic Sea.

During the last decades, the collapse of sprat (*Sprattus sprattus*) and anchovy (*Engraulis encrasicolus*) stocks in the Adriatic affected the species stocks of the entire Mediterranean and was associated with the decrease of surface temperature resulting from climatic anomalies (Regner, 1996; Salat, 1996; Bombace, 2001; Azzali *et al.*, 2002). Similarly, during the 2001 winter, climate-induced low surface temperatures led to the decline of sardines (*Sardinella aurita*) and phytoplankton blooms (Guidetti *et al.*, 2002).

By altering oceanographic properties like seawater temperature, salinity, water transparency and deep water oxygen saturation, climate change could impact the entire Adriatic Sea ecosystem (Zore-Armanda *et al.*, 1987; Zore-Armanda, 1991; Russo *et al.*, 2002).

Global warming may promote the development of toxic dinoflagellates like *Gymnodinium catenatum* which is responsible for frequent Mediterranean toxic events, causes paralytic shellfish poisoning (PSP) and may alter the marine ecosystem (Garcés *et al.*, 2000; Taleb *et al.*, 2001; Vila *et al.*, 2001; Calbet *et al.*, 2002; Gomez, 2003). According to Calbet *et al.* (2002), the occurrence of *Gymnodinium catenatum* (toxic dinoflagellate) in the Alboran Sea reduced the grazing impact of mesozooplankton on the microbial communities and may have altered the Mediterranean pelagic food web.

Gomez & Claustre (2003) and Polat (2004) suggest that the presence of new warm-water dinoflagellate species in the Mediterranean Sea, like *Asterodinium libanum*, *Asterodinium gracile* and *Citharistes regius* is likely to be associated with the warming of Mediterranean waters. A species of a similar genus, *Ostreopsis armata*, was recently observed (summer 2005 and 2006) in the Ligurian Sea where it repeatedly bloomed and apparently triggered respiratory diseases in humans (details in Occhipinti-Ambrogi, 2007).

Meteorological anomalies can significantly alter ecosystems and cause mass mortality episodes. In the eastern Mediterranean Sea, a climatic event, called the Eastern Mediterranean Transient (EMT), was correlated with local meteorological anomalies (reduced precipitation, change in wind patterns and cold winters) (Klein *et al.*, 1999) and resulted in a drastic alteration of faunal abundance and diversity (Danovaro *et al.*, 2001). By modifying the physico-chemical characteristics of the deep waters, this temperature shift significantly and rapidly affected deep-sea nematode diversity (Danovaro *et al.*, 2004). Following the 1994–1995 period, when the temperature recovered, only some marine faunal species recovered (Danovaro *et al.*, 2004). These observations give us a better vision of the potential large-scale consequences of global warming.

increase of diseases and pathogens

Since warmer temperatures are known to favour the presence of pathogens, epidemiological outbreaks are likely to become more severe and frequent with the warming of Mediterranean waters (Gantzer *et al.*, 1998; Harvell *et al.*, 1999, 2002; Marcogliese, 2001; Drake *et al.*, 2007). According to CIESM (2004) global warming could lead to the development of tropical and subtropical pathogens across the Mediterranean Sea. Along the Ligurian Sea, the massive development of a cyanobacterium combined with warm water, caused several populations of the zoanthid *Parazoanthus axinellae* to decline since 2000 (Cerrano *et al.*, 2006). This species has been replaced by an incrusting thermophilic sponge (*Crambe crambe*) which quickly colonized the niche deserted by *Parazoanthus* (Cerrano *et al.*, 2006).

Similarly, the thermophilic bacteria *Vibrio shiloi*, was involved in the mortality episode of the Mediterranean coral *Oculina patagonica* (Kushmaro *et al.*, 1998) and the 1999 mass mortality event in the Ligurian Sea was induced by the combination of a temperature shift with the growth of opportunistic warm-water pathogens (Cerrano *et al.*, 2000).

Simmonds & Mayer (1997) provided a tentative link between reduced nutrient input to the western Mediterranean basin (resulting from reduced rain fall) and the initiation of the striped dolphin (*Stenella coeruleoalba*) mass mortality in 1990. This is discussed further below.

other expected changes

Increased concentration of atmospheric anthropogenic CO_2 and climate change is likely to alter marine ecosystems in several other ways. As temperature increases, the oxygen solubility decreases and fish metabolism accelerates (Green & Carritt, 1967; Pörtner & Knust, 2007). Since the demand for oxygen and food will be enhanced in order to support higher metabolic rates, the decreased concentration of dissolved oxygen will thus affect fish growth and breeding capacity, and could lead to the extinction or migration (to cooler waters) of some fish species (Pörtner & Knust, 2007). Furthermore, enhanced fish metabolic rates and food consumption resulting from higher seawater temperatures may increase fish pollutant uptake (e.g. mercury) which will then be transferred into higher levels of the food chain (Harris & Bodaly, 1998).

In addition, the rise of atmospheric CO_2 could increase the acidity of seawater and therefore reduce the saturation state of $CaCO_3$ species in the oceans, namely calcite and aragonite (Caldeira & Wickett, 2003; Orr *et al.*, 2005). The marine species most likely to be affected by this acidification will be small and thin-shelled organisms that use $CaCO_3$ such as calcifying plankton (e.g. coccolithophores), coralline algae, pteropod molluscs and coral polyps (e.g. reef-building scleractinian corals) (Kleypas *et al.*, 1999; Riebesell *et al.*, 2000; Feely *et al.*, 2004). By reducing the level of calcium carbonate saturation, ocean acidification will affect the process of calcification of some marine key organisms. Feely *et al.* (2004) argue that the calcification rate of multiple taxa will be affected, from single celled protists to reef-building corals—and across all CaCO mineral phases. Cephalopods may also be particularly sensitive and this is described in Table 2 at the end of this paper. According to a study recently carried out by The Royal Society (2005), the plankton calcification process could become very limited and a large portion of marine life could then disappear by 2100.

The seawater acidification phenomenon, which is responsible for nanism (a genetic anomaly resulting in short stature) and malformation symptoms in several phytoplankton species (Feely *et al.*, 2004), can also have an impact on the reproductive patterns of fish (Stanley, 1984).

According to Caldeira & Wickett (2003) and Feely *et al.* (2004), the expected change in pH will be greater than any other pH variations observed in the fossil record over the last 200–300 million years. Manipulative experiments showed that a three-month reduction of pH by 0.7-unit reduced mussel metabolism and growth (Michaelidis *et al.*, 2005). Similarly, a six-month, 0.03-unit pH reduction, which corresponds to a 200-ppm increase in atmospheric CO_2, lowered gastropod and sea urchin growth and survival (Shirayama & Thornton, 2005). A study by Alvarez *et al.* (2005) shows that, although ocean uptake of carbon dioxide for the Mediterranean appears small in terms of global ocean uptake, 'the impact on local carbonate chemistry will be large.'

In addition to this process of ocean acidification, changes in marine ecosystems due to global warming (e.g. water temperature, algal bloom enhancement and water colour) might affect the visual sensitivity of fish (spectral sensitivity) (Archer *et al.*, 2001).

Several points discussed in this section are likely to be relevant to a broad variety of marine species including key species in Mediterranean ecosystems, with significant consequences for foodweb structures, marine system functions and ecosystem equilibrium (Petchey *et al.*, 1999; Sanford, 1999; Schiel *et al.*, 2004). Such foodweb alterations are likely to produce significant cascade effects on marine biodiversity including impacts on species of higher trophic levels, such as cetaceans.

Climate change impacts on cetaceans

The distribution of cetaceans, which have a major influence on marine community function and structure (e.g. Katona & Whitehead, 1988; Bowen, 1997; Jones *et al.*, 1998), is closely related to environmental parameters such as oceanographic features and food availability (Millot & Taupier-Letage, 2004). According to MacGarvin & Simmonds (1996), they are not likely to be able to adapt to rapid shifts in temperatures and environmental conditions, and climate change may represent the most serious long-term threat to cetaceans (Burns, 2001). Although lower trophic levels are the most likely to be altered, cetaceans could be affected by global warming in a variety of ways (Figure 2; Table 2) (e.g. Reeves, 1991; Fisher *et al.*, 1994; Agardy, 1996; IWC, 1997; European Community, 1999; Hardwood, 2001; Simmonds & Nunny, 2002; Gambaiani *et al.*, 2005; Learmonth *et al.*, 2006; Simmonds & Isaac, 2007).

change in food supply

The distribution, abundance and migration of cetaceans is strongly influenced by prey availability (e.g. Kenney *et al.*, 1996) and cetaceans which are confined in restricted habitat,

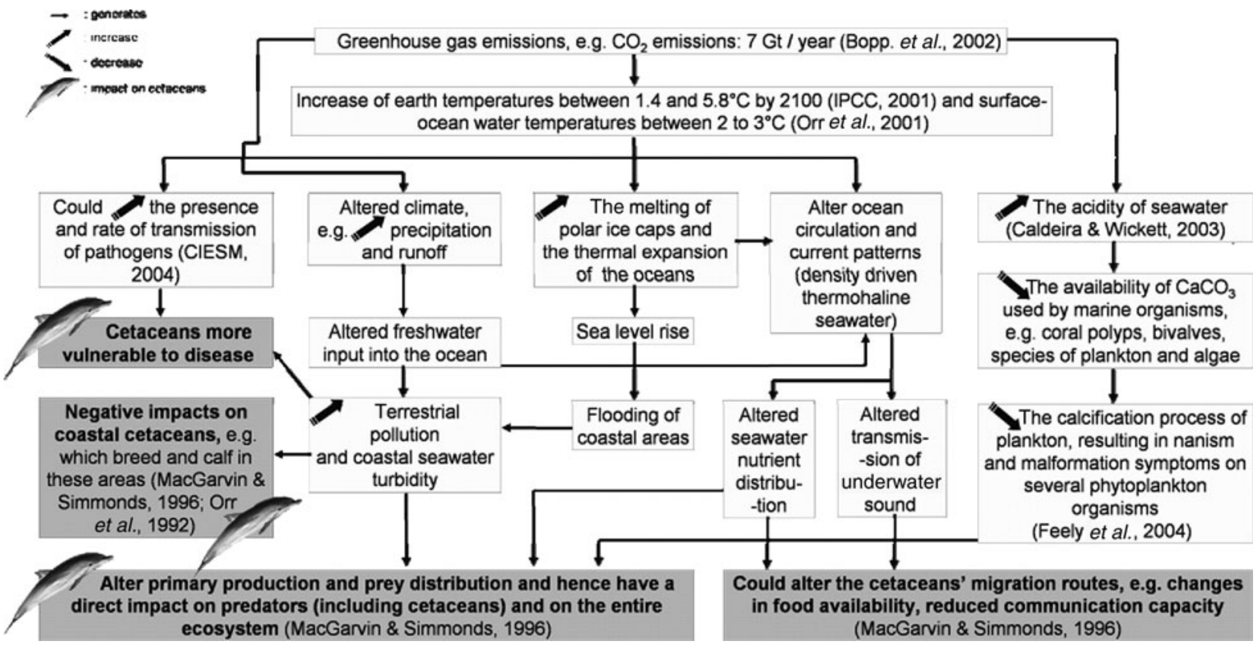

Fig. 2. Overview of the potential impacts of global warming on marine life, including cetaceans (from Gambaiani *et al*., 2005).

with limited ranges, are likely to be most vulnerable to climate change (e.g. Learmonth *et al*., 2006; Simmonds & Isaac, 2007).

Change in key prey species distribution is the main driving factor defining geographical range and habitat preference in cetaceans (e.g. Evans, 1971; Wells *et al*., 1990; Hanson & Defran, 1993; Simmonds, 1994; Agardy, 1996; Maze & Würsig, 1999).

For instance, in the eastern North Pacific Ocean, an increase in seawater temperature combined with a change in oceanographic conditions is thought to have led to the death of hundreds of grey whales (*Eschrichtius robustus*) as the result of a decline in their prey species (Grebmeier & Dunton, 2000; Moore *et al*., 2003; Gulland *et al*., 2005). In the Mediterranean Sea, the decline of several cetacean populations has been associated with the reduction of prey resources (Perrin, 1989; UNEP/IUCN, 1994; Reeves *et al*., 2003; Reeves & Notarbartolo di Sciara, 2006).

Odontocete prey species such as pilchard (*Sardina pilchardus*) are affected by climate change (Southward *et al*., 1988; Garcia & Palomera, 1996; Regner, 1996; Bearzi *et al*., 2003). Pilchards have been shown to be a key prey species for common dolphins off the Portuguese coast (Silva, 1999). In addition, cephalopods, which represent the main food supply for numerous Mediterranean cetacean species (Wurtz & Marrale, 1991; Bompar, 2000; Bearzi *et al*., 2003) seem to be particularly vulnerable to environmental changes including pH and temperature (Sims *et al*., 2001; Pierce & Boyle 2003; Arkhipkin *et al*., 2004) (Table 2).

In the Adriatic Sea, climatic shifts are suggested to have altered the distribution of the key prey species of common dolphins (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) (Blanco *et al*., 2001; Bearzi *et al*., 2003). In particular, the climate-induced increase in abundance of thermophilic species such as round sardinella and jellyfish may have caused the European anchovy (*Engraulis encrasicolus*) population to decrease (Regner, 1996).

Shifts in prey species availability may force cetaceans to change their feeding strategies and spend more time and energy foraging, which could have drastic consequences on their health and could affect their immune systems (Northridge, 1984; Shane, 1990; Bräger, 1993; Smith & Whitehead, 1993; Agardy, 1996; Stern, 1996; Bearzi, 2002). A high proportion of time and effort devoted to feeding-related activities was recorded in Mediterranean bottlenose dolphins in the northern Adriatic Sea as a response to environmental changes and reduced prey availability (Politi, 1998; Bearzi *et al*., 1999). Consequently, the time dedicated to socializing and breeding is reduced, with negative consequences on cetacean reproductive success (Valiela, 1995; Bearzi, 2002). The fact that climate change impacts can lead to reduced prey availability and subsequently affect the health, physical strength and abundance of cetacean populations, has been observed in bottlenose dolphins in the eastern Ionian Sea (Politi *et al*., 2000; Politi & Bearzi, 2004).

Aguilar & Raga (1993) and Simmonds & Mayer (1997) have suggested that the mass mortality of thousands of striped dolphins (*Stenella coeruleoalba*) during the 1990–1992 morbillivirus epizootic might have been caused by the unusual warm and dry winter of 1989–1990 that led to abnormally warm water temperatures and low rainfall. This phenomenon resulted in reduced nutrient input into the eastern Mediterranean and thus low productivity (Simmonds & Mayer, 1997). This led to the decline of the dolphin's common prey and explains why many of the dolphin carcasses showed depleted body fat reserves (Aguilar *et al*., 1991).

Similarly, during a survey carried out in Corsica, Dhermain (2003) observed fewer bottlenose dolphins in coastal waters than usual. The excessively hot 2003 summer, which resulted in abnormally high coastal water temperatures, could explain the migration of bottlenose dolphins toward the open sea. Such exceptional meteorological events may illustrate how an increase of temperature could impact on cetaceans.

Moreover, global warming is likely to encourage the spreading of viruses and pathogens and may promote epizootic events like morbillivirus infections (Agardy, 1996), which have also been identified in the endangered

Table 2. Impact of climate changes on cetaceans around the world.

Global warming-induced changes	**Impacts on marine mammals with some examples of species most likely to be, or, already affected**	
Seawater temperature	Directly affected: • Endangered, young animals, species with low mobility, restricted distribution, low thermal tolerance like vaquitas (*Phocoena sinus*) in the Gulf of Mexico; Arctic bowhead whales (*Balaena mysticetus*); Arctic belugas (*Delphinapterus leucas*); narwhals (*Monodon monoceros*); finless porpoises (*Neophocaena phocaenoides*), tropical dolphins, humpback whales (*Megaptera novaeangliae*) in the Indian Ocean, Mediterranean fin whales (*Balaenoptera physalus*) and river dolphins (IWC, 1997; Bannister, 2002; Würsig *et al.*, 2002; Simmonds, 2004; COSEWIC, 2005; Laidre & Heide-Jorgensen, 2005; Robinson *et al.*, 2005; Learmonth *et al.*, 2006; Simmonds & Isaac, 2007) • Animals like bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico, living in coastal zones where seawater temperature variation is enhanced (IWC, 1997) • Cold-water species like white-beaked dolphins (*Lagenorhynchus albirostris*) in north-western Scotland whose relative abundance and occurrence decreased whereas warm-water common dolphins (*Delphinus delphis*) increased in this region (MacLeod *et al.*, 2005) • Long-finned pilot whale (*Globicephala melas*) population structure in the North Atlantic and short-finned pilot whales (*Globicephala macrorhynchus*) distribution in Japan (Fullard *et al.*, 2000) Effects on prey availability affecting the distribution and geographical range of: • Long-finned pilot whales in the Faeroe Islands (Bjorge, 2002) • Bottlenose dolphins in north-east Scotland (Wilson *et al.*, 2004) Effects on prey availability affecting the reproductive success of: • North Atlantic right whales (*Eubalaena glacialis*) (Greene & Pershing, 2004)	• North-east Atlantic fin whales (Lockyer, 1986) • Humpback whales (Wiley & Clapham, 1993) • Harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy (Read & Gaskin, 1990) Effects on reduced prey availability leading to: • Increased vulnerability to disease particularly for species at the limit of their thermal tolerance (Würsig *et al.*, 2002; Lafferty *et al.*, 2004) • Increase of mass mortality events like morbillivirus that affected Mediterranean striped dolphins (*Stenella coeruleoalba*) (Aguilar & Raga, 1993; Cebrian, 1995; Harvell *et al.*, 1999; Kennedy, 1999; Geraci & Lounsbury, 2002) • Higher exposure to contaminants stocked in blubber and mobilized during starvation (Aguilar *et al.*, 1999), that alter reproductive, endocrine and immune systems (Fuller & Hobson, 1986; Aguilar & Borrell, 1994; Ross *et al.*, 2000) • Stranding of hundreds of grey whales (*Eschrichtius robustus*) in eastern America (Grebmeier & Dunton, 2000; Moore *et al.*, 2003; Gulland *et al.*, 2005) • Episodic shifts in cetacean populations' abundance and distribution in the Gulf of Maine. Concerned species: humpback and fin whales replaced by right and sei whales (*Balaenoptera borealis*); white-beaked dolphins (*Lagenorhynchus albirostris*) replaced by Atlantic white-sided dolphins (*Lagenorhynchus acutus*); and harbour porpoise (*Phocoena phocoena*) (Kenney *et al.*, 1996; Palka *et al.*, 1997) • Episodic shifts in the inshore incidence of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) in British Columbia (Morton, 2000) • Disappearance of common dolphins (*Delphinus delphis*) along the north-eastern coast of Florida (Caldwell & Caldwell, 1978)
Precipitation and extreme weather occurrence	Effects of warmer seawater temperature and nutrient enrichment due to increased runoff: • Increase in the frequency and strength of toxic algal bloom episodes triggering lethal poisoning in marine mammals (Hernández *et al.*, 1998; Burns, 2002; Geraci & Lounsbury, 2002) • Increase in eutrophication events affecting marine organisms dynamics like phytoplankton in the North Sea (Edwards *et al.*, 2001)	Effects of pollutants inputs into coastal waters due to increased runoff and flooding events: • Impacts on coastal marine mammals and other organisms (including prey species) (e.g. MacGarvin & Simmonds, 1996; Orr *et al.*, 1992; Learmonth *et al.*, 2006) Effects on oceanic properties (coastal waters salinity, circulation, etc) affecting: • The distribution and abundance of cetaceans' prey species (e.g. MacGarvin & Simmonds, 1996; Learmonth *et al.*, 2006)
Sea level rise	Flooding of coastal habitats and impacts on species that depend on coastal areas (as breeding, nursing, feeding, mating, resting zones) like: • Mediterranean monk seals (*Monachus monachus*) breeding in caves or on small beaches (Harwood, 2001; Würsig *et al.*, 2002)	• Grey and humpback whales (IWC, 1997)
Ocean circulation	Changes in current patterns and oceanic fronts directly affecting: • The distribution of the majority of tropical and temperate cetaceans (Worms *et al.*, 2005; Learmonth *et al.*, 2006) like sperm whales associated with the Antarctic convergence in the Southern Ocean (Boyd, 2002)	Changes in water mass formation, mixing and upwelling pattern affecting: • Marine biodiversity and ecosystems (IPCC, 2001a) • The distribution, abundance and migration of plankton, fish and cephalopods (e.g. Planque & Taylor, 1998; Waluda *et al.*, 2001; Walther *et al.*, 2002) affecting cetaceans like minke whales (Bjorge, 2002)

Continued

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Table 2. *Continued.*

Global warming-induced changes	Impacts on marine mammals with some examples of species most likely to be, or, already affected	
Salinity	Direct affects on cetaceans epidermis generating: • More important skin lesions in bottlenose dolphins living in salted and cold waters (Learmonth *et al.*, 2006) • Animal increased stress and susceptibility to diseases or anthropogenic impacts (Wilson *et al.*, 1999)	Effects on prey species through changes in oceanic properties or low salinity tolerance like: • Most cephalopod species (e.g. De Heij & Baayen, 2005) • Coastal phytoplankton of the Antarctic peninsula (Moline *et al.*, 2004)
Seawater pH	Increased CO_2 affecting metabolic function, growth and reproduction of water-breathing organisms (e.g. Pörtner *et al.*, 2004; Orr *et al.*, 2005; Royal Society, 2005)	• High metabolic rate species like ommastrephid squids (e.g. *Illex illecebrosus*) (Learmonth *et al.*, 2006)
Large-scale atmospheric patterns occurrence and strength (e.g. North Atlantic Oscillation (NAO), El Niño, Southern Oscillation, Pacific Decadal Oscillation (PDO))	Increase in frequency of large-scale atmospheric events (Timmermann *et al.*, 1999) affecting the distribution, growth, abundance and recruitment of marine organisms (IPCC, 2001a; Stenseth *et al.*, 2002) including: • Market squid (*Loligo opalescens*), a short-finned pilot whales' prey (Shane, 1995) • North Atlantic cod (*Gadus morhua*) (Stenseth *et al.*, 2002) • North Atlantic copepods *Calanus finmarchicus* and *Calanus helgolandicus* (Planque & Taylor, 1998; Beare *et al.*, 2002; Beaugrand & Ibanez, 2004) Large-scale atmospheric events' impacts on prey availability and thus affecting: • Community structure of short-finned pilot whale (*Globicephala macrorhynchus*) being replaced by Risso's dolphins (*Grampus griseus*) in southern California (Shane, 1995; Würsig *et al.*, 2002) and in the Gulf of Mexico (Jefferson & Schiro, 1997)	• Sperm whale (*Physeter macrocephalus*) reproductive success in the Galapagos (Whitehead, 1997) • Dusky dolphins (*Lagenorhynchus obscurus*) reproductive success in Peru (Manzanilla, 1989) • Short-beaked common dolphins (*Delphinus delphis*) and other Delphinidea distribution in New Zealand (Gaskin, 1968; Neumann, 2001) • Southern right whales breeding success (Leaper *et al.*, 2006) • Californian coastal bottlenose dolphins geographical range (Wells *et al.*, 1990; Würsig *et al.*, 2002) • Grey whale high mortality rate and low recruitment in the Pacific Ocean (Le Boeuf *et al.*, 2000) • Pacific killer whales (*Orcinus orca*) and Atlantic bottlenose dolphins social organization and behaviour (Lusseau *et al.*, 2004) • North Atlantic right whales breeding success (Simmonds & Isaac, 2007) • Sperm whale in the north-east Atlantic (Robinson *et al.*, 2005) • Probably, the North Atlantic cetaceans in general, in response to the NAO (Learmonth *et al.*, 2006)

Mediterranean monk seal (*Monachus monachus*) (Van de Bildt *et al.*, 1999). A worldwide increase in mass mortality events in marine mammals has been reported by Simmonds & Mayer (1997).

It is interesting to note that, as cetaceans are long-lived, slow-reproducing animals (generally producing one offspring per female every 2–3 years), when a population is severely diminished by a virus or other agents, recovery may be slow and such species can relatively easily become endangered (Dhermain *et al.*, 2002; Reeves *et al.*, 2003).

According to Greene & Pershing (2004), in the North Atlantic Ocean, the effects of global warming on the abundance of *C. finmarchicus* strongly influence right whale (*Eubalaena glacialis*) calving rates. A similar situation is likely to take place in the Mediterranean. For instance, *Meganyctiphanes norvegica*, which constitutes the only known food supply of the fin whales (*Balaenoptera physalus*) in this region, is at the northern limit of its distribution (Besson *et al.*, 1982; Viale, 1985; Orsi Relini & Giordano, 1992; Orsi Relini *et al.*, 1994; Gannier, 1995, 1997; Forcada *et al.*, 1996; Astruc & Beaubrun, 2001; Notarbartolo di Sciara *et al.*, 2003) and thus, in case of unsuitable environmental properties, will not be able to move northward because of the physical land barrier.

The distribution and abundance of this euphausid are correlated with specific hydrobiological parameters (e.g. seawater temperature, salinity, food availability and current patterns) (Pustelnik, 1976; De la Bigne, 1985; Macquart-Moulin & Patriti, 1996; Velsch, 1997). Climate change-induced alteration of ocean circulation is likely to modify larval transport processes, species dispersal and recruitment, and impact krill population dynamics (Harley *et al.*, 2006).

According to Einarsson (1945), in the north Atlantic, the optimal temperature range of *Meganyctiphanes norvegica* is between 2 and 15°C with a high mortality rate above 15°C (Buchholz *et al.*, 1995). This thermal limit is 18°C for the Mediterranean population (Fowler *et al.*, 1971). Salinity change is also likely to affect this species which has its tolerance limit at 20–24 ppm (Forward & Fyhn, 1983).

Whereas, temperature warming in the north-east Atlantic has led to the migration of several marine organisms to northern latitudes (e.g. Beaugrand *et al.*, 2002), in the Mediterranean Sea, *Meganyctiphanes norvegica* will not be able to extend its range northward because of the land barrier and is likely to share its environment with more thermophilic invasive species in the future.

Furthermore, calcifying organisms including some phyto- and zooplankton species are likely to be affected by acidification (Royal Society, 2005) and a possible temporal mismatch may result between *Meganyctyphanes norvegica* and phytoplankton blooms, its food supply, with protential consequences for predators including the endangered bluefin tuna (*Thunnus thynnus*), albacore tuna (*Thunnus alalunga*) (Quynh, 1978), squid (*Illex coindetii*) (Sanchez, 1982) and the Mediterranean fin whale population.

Mediterranean fin whale distribution can be expected to be affected by food availability (Littaye *et al.*, 2004) and since

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Mediterranean fin whales are genetically and reproductively isolated from those of the Atlantic (Bérubé *et al.*, 1998), they are regarded as more vulnerable to environmental pressures, including global warming (Dhermain *et al.*, 2002).

By affecting the distribution and abundance of cetacean prey species, climate change is likely to trigger dietary competition between species, and could then cause inter- and intra-species competition between Mediterranean cetaceans. This is particularly true for striped dolphins and common dolphins (Aguilar, 2000), whose food web dynamics have been affected by recent temperature changes (Bearzi *et al.*, 2003).

In addition, a decrease of prey species may increase cetacean mortality rates and vulnerability to diseases as a consequence of reduced immune function, as in the Mediterranean striped dolphin epizootic outbreak in the 1990s (Aguilar & Raga, 1993; Bearzi, 2002).

CLIMATE CHANGE COMBINED WITH FISHERIES PRESSURE

The combination of climate-induced impacts with other anthropogenic impacts like overfishing is likely to impact cetaceans (CIESM, 2000; Bearzi, 2002). Several cetacean species such as coastal bottlenose dolphins and common dolphins are already competing with fishermen for prey species exploited by fisheries (Bearzi, 2002; Abad *et al.*, in press). As previously observed prey species distribution and abundance could be severely affected by global warming. The diminution of fish stocks is likely to result in a stronger competition with fishermen and in higher risks of harassment of dolphins by fishermen (Northridge, 1984; UNEP/IUCN, 1994; Fertl & Leatherwood, 1997; Bearzi, 2002).

According to Bearzi *et al.* (2004), global warming is today a major concern for Mediterranean common dolphin which feed on species that are targets of fisheries, such as European anchovy, European pilchard (*Sardina pilchardus*), round sardinella (*Sardinella aurita*) and sprat (*Sprattus sprattus*) (Orsi Relini & Relini, 1993; Boutiba & Abdelghani, 1995; Birkun, 2002; Bearzi *et al.*, 2003) and that could be affected by global warming. For instance, in the Black Sea, the two mass mortality events involving common dolphins (*Delphinus delphis*), in 1990 and 1994, coincided with the decline of European sprat and anchovy stocks, their main prey species (Krivokhizhin & Birkun, 1999; Birkun, 2002). The combination of several factors, including seawater eutrophication, which is likely to be encouraged with global warming, and over-fishing, were responsible for the rapid decline of sprats and anchovies (Zaitsey & Mamaev, 1997).

OTHER POSSIBLE CLIMATE CHANGE-INDUCED IMPACTS ON CETACEANS

Climate change is likely to affect cetacean populations in several other ways (Figure 2). For instance, species that breed, feed and calve in coastal areas are more likely to be impacted by climate change which is likely to generate coastal inundations and reduce water quality by releasing pollutants into the marine environment (Orr *et al.*, 1992; Agardy, 1996; Simmonds & Nunny, 2002).

Changes in current patterns could alter cetacean migration routes and affect the transmission of sound and therefore the cetaceans' communication capacity (Agardy, 1996; MacGarvin & Simmonds, 1996; IWC, 1997).

Moreover, a change in environmental parameters like salinity might trigger more physiological stress (possibly presenting as skin lesions) and make cetaceans more susceptible to diseases or anthropogenic pressures (Wilson *et al.*, 1999; Learmonth *et al.*, 2006). These pressures, including incidental capture in fishing nets, noise and chemical pollution could have synergistic or cumulative impacts with climate change.

Finally, the increased frequency of poisonous algal blooms, like dinoflagellates, which often generate brevetoxins, has been correlated with the collapse of several marine species including cetaceans like striped dolphins in the Mediterranean Sea (Geraci *et al.*, 1989; Fitzgerald, 1991; Burns, 1998, 2001, 2002; Balmer-Hanchey *et al.*, 2003; Danovaro, 2003). Global warming, which is likely to encourage this phenomenon, could indirectly, yet profoundly affect cetaceans.

CONCLUSION

This review illustrates the different linkages existing between climate and biodiversity. It illustrates the urgent necessity for more integrated regulations for the protection of marine biodiversity. Similarly, the development of exemplary and reproducible projects aiming to reduce greenhouse gas emissions should be supported.

By influencing seawater properties, climate change can alter ecological interactions between trophic levels and is likely to disrupt overall ecosystem function. Climate change is affecting and will continue to affect marine ecosystems. Although recent climatic anomalies represent only a small part of the forecasted changes, they have already generated important responses in marine ecosystems. Marine biodiversity, including cetaceans, is highly vulnerable to environmental alteration, and can be significantly and irremediably affected by even small temperature changes. Combined with other anthropogenic pressures, climate change is likely to impact the survival of some rare and endangered marine flora and fauna, and may also threaten many other species. For example, some cetacean species that inhabit restricted geographical zones, with no option to shift their range, or those unable to effectively switch prey species if necessary may be adversely affected by climate change. As well as impacts on populations of marine biota, the physiology of individual organisms may also be severely affected, either directly or indirectly, by climate change, for example through ocean acidification.

Today, the International Whaling Commission considers global warming as a major issue (IWC, 1997) and is in the process of establishing a special workshop to examine its impacts and as Baker (in Burns, 2001) said: 'While we debate the limits that should be placed on whaling in order to protect the status of the stocks, a silent menace threatens to destroy the populations we strive to protect'. Climate change must be considered as a priority and uncertainties concerning its future impacts on biodiversity depend on the social and economic response of our societies to global warming.

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