



Impacts of climate change on European marine ecosystems: Observations, expectations and indicators

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ABSTRACT

The Northern Hemisphere has been warmer since 1980 than at any other time during the last 2000 years. The observed increase in temperature has been generally higher in northern than in southern European seas, and higher in enclosed than in open seas. Although European marine ecosystems are influenced by many other factors, such as nutrient enrichment and overfishing, every region has shown at least some changes that were most likely attributable to recent climate change. It is expected that within open systems there will generally be (further) northward movement of species, leading to a switch from polar to more temperate species in the northern seas such as the Arctic, Barents Sea and the Nordic Seas, and subtropical species moving northward to temperate regions such as the Iberian upwelling margin. For seas that are highly influenced by river runoff, such as the Baltic Sea, an increase in freshwater due to enhanced rainfall will lead to a shift from marine to more brackish and even freshwater species. If semi-enclosed systems such as the Mediterranean and the Black Sea lose their endemic species, the associated niches will probably be filled by species originating from adjacent waters and, possibly, with species transported from one region to another via ballast water and the Suez Canal. A better understanding of potential climate change impacts (scenarios) at both regional and local levels, the development of improved methods to quantify the uncertainty of climate change projections, the construction of usable climate change indicators, and an improvement of the interface between science and policy formulation in terms of risk assessment will be essential to formulate and inform better adaptive strategies to address the inevitable consequences of climate change.

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1. Introduction

Globally, the marine environment is changing rapidly (e.g. Johnson et al., 2011-this issue; Menge et al., 2011-this issue; Schiel, 2011-this issue; Wernberg et al., 2011-this issue; all this volume). During the last 10–15 years, sea water temperatures throughout much of the globe have changed at unprecedented rates: sea ice cover in the Arctic is rapidly disappearing; melting of glaciers and the Greenland ice cap is accelerating; the volume of Antarctic ice sheets is reducing; sea levels are rising and seas are getting stormier; precipitation is more variable with more frequent intense rainfall events; hurricane intensity appears to be greater and springtime is occurring earlier (Solomon et al., 2007; IPCC, 2007; Hoegh-Guldberg and Bruno, 2010). Many of these events are thought to be predominantly a consequence of climate change (IPCC, 2007; Hoegh-Guldberg and Bruno, 2010). Although marine species and ecosystems have responded to such variations in their environment throughout evolutionary history, a primary concern is the rapid rate of change currently observed (Root et al., 2003).

Regional changes are often more relevant in the context of ecological responses than global averages (Walther et al., 2002). European seas are disproportionately affected by global warming; 10 of the 18 large marine ecosystems (LMEs) in the World have recently experienced fast to super-fast warming (Belkin, 2009; Table 1). Comparison between fast-warming European LMEs and the biomass yields of fisheries between 1982 and 2006 showed contrasting relationships (Sherman et al., 2009). Whilst yields increased in the northern seas, (i.e. Norwegian Sea, Faroe Plateau and Iceland Shelf), they decreased in more southern open (i.e. North Sea, Celtic Biscay, and Iberian Coastal) and enclosed (i.e. Baltic, Mediterranean and Black) seas. These differences across European seas are considered in northern seas to be the result of climate-induced improvement in feeding conditions for zooplankton and fish in northern seas and an impoverishment of these conditions in the south (Sherman et al., 2009).

Climate-induced changes strongly differ throughout the globe, especially along a latitudinal gradient. Warming will be more pronounced at the poles than at the equator (MacDonald et al., 2005). The responses of climate change are expected to differ for different marine systems (Hoegh-Guldberg and Bruno, 2010; McGinty et al., 2011-this issue, this volume). For example, whilst open oceans are more affected by the influence of wind on the timing and strength of stratification, coastal areas are expected to be more vulnerable to the effects of wind via storm surges. Polar regions will experience changes in ice cover. Seas at the same latitude are expected to respond differently to climate change due to their region-specific abiotic characteristics such as basin depth and configuration, salinity regime and current pattern, and biotic attributes including biogeographical setting, biodiversity and food-web structure.

The response of marine systems to climate change will also depend on interactions with other human-induced changes in the marine

environment. For example, fishing has reduced the number of large fish at higher trophic levels worldwide (Pauly et al., 1998; Jackson et al., 2001; Myers and Worm, 2003) whilst increasing agricultural, industrial and household activities have resulted in nutrient enrichment of many coastal regions (Schindler, 2006). Mieszkowska et al. (2009) have recently reviewed the effects of climate change and overfishing on commercially exploited cod in the Atlantic. These and other global changes, such as ocean acidification (The Royal Society, 2005) and the introduction of non-native species (Doney, 2010), are likely to result in more fragile marine ecosystems, which will challenge the effectiveness of management strategies that may be implemented to reduce the impacts of climate change (Hoegh-Guldberg and Bruno, 2010).

Our paper summarises the current state of knowledge with regard to general and region-specific impacts of climate change on 10 European marine systems: the Arctic Ocean, North-east Atlantic Ocean, Barents Sea, Nordic Seas, North Sea, Baltic Sea, Celtic-Biscay Shelf, Iberian upwelling margin, Mediterranean Sea, and Black Sea (Fig. 1). Results from earlier long-term studies of European seas are used to examine

Table 1
Observed and predicted changes in SST of European Seas.

European Sea	Observation/prediction	Reference
Arctic Ocean		
ΔSST observed	ca. +0.2 °C per decade (1965–95)	Steele et al., 2008
ΔSST predicted	+4 to 7 °C (1990s–2090s)	ACIA, 2005; IPCC, 2007
Barents Sea		
ΔSST observed	+0.12 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+1 to 2 °C (1990s–2080s)	Furevik et al., 2002
Nordic Seas		
ΔSST observed	+0.85 °C (1982–2006)	Belkin, 2009 (Norwegian Sea)
ΔSST predicted	+1 to 2 °C (1990s–2080s)	Furevik et al., 2002
NE Atlantic		
ΔSST observed	+1 °C (1975–2005)	Philippart et al., 2007
ΔSST predicted	+2 °C (1990s–2090s)	This paper
North Sea		
ΔSST observed	+1.31 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+0.8 °C (1990s–2040s)	Clark et al., 2003
Baltic Sea		
ΔSST observed	+1.35 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+2 to 4 °C (1990s–2090s)	Graham et al., 2008
CB Shelf		
ΔSST observed	+0.72 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+1.5 to 5 °C (1990s–2090s)	This paper
Iberian upwelling		
ΔSST observed	+0.68 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+1.4 to 2.4 °C (1960/1990–2070/2100)	This paper
Mediterranean		
ΔSST observed	+0.71 °C (1982–2006)	Belkin, 2009
ΔSST predicted	+2.6 °C (1961/1990–2070/2099)	Somot et al., 2008
Black Sea		
ΔSST observed	+0.96 °C (1982–2006)	Belkin, 2009
ΔSST predicted		

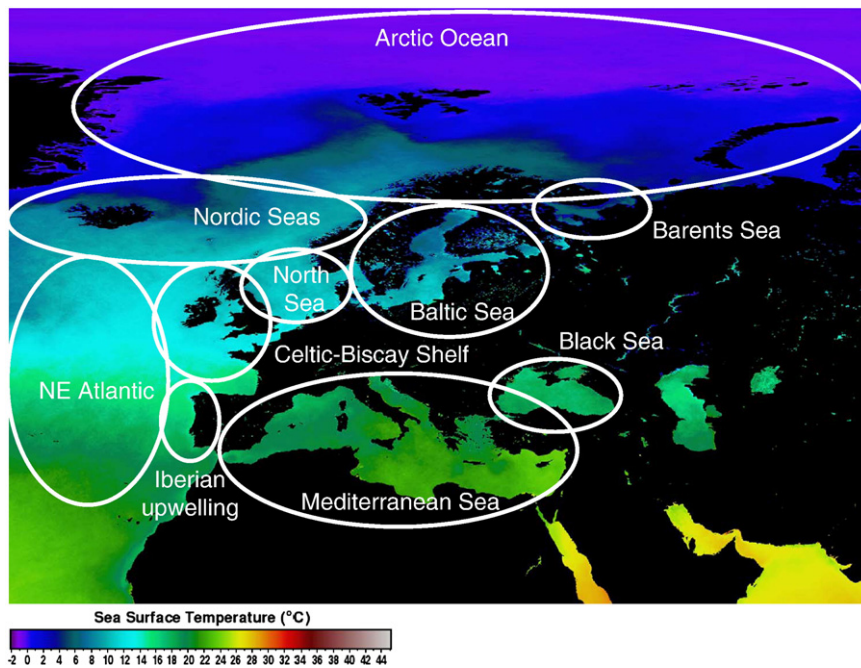


Fig. 1. Annually averaged sea surface temperature in 2009 as measured by MODISA satellite (4 km resolution, 11:00 daytime) (oceancolor.gsfc.nasa.gov), and locations of main European marine systems discussed in this paper.

past changes, put recent rapid changes into context, and to forecast likely future ecosystem responses to climate change. Based on general and system-specific observations and expectations, a number of abiotic and biotic indicators of the impacts of climate change are proposed. Monitoring of climate change indicators over appropriate time scales will be essential to formulate and inform better adaptive strategies to address the inevitable consequences of climate change.

2. System-specific signals and projections

In general for the European Seas considered here the pattern of sea temperature over the last century has fluctuated from generally cold conditions in the early 1900s to a warm period from the 1920s to the 1950s, cool again through the 1960s and 1970s, followed by recent warming that commenced in the mid 1980s (Johannessen et al., 2004; Fig. 2).

2.1. Arctic Ocean

The Arctic Ocean has shown the general pattern noted above, with a recent increase in annual mean air temperature that is 50% higher than in the area between Iceland and the equator (ACIA, 2005). This recent warming has resulted from changes in atmospheric pressure systems that have led to an increased flow of warm air from the south (Overland et al., 2004). In addition, warming (over 1 °C) has occurred at intermediate depths in the Arctic Ocean, especially in the Eurasian Basin, due to increased inflow of warm Atlantic water (Polyakov et al., 2005). Recent projections of future climate scenarios indicate continued warming in the Arctic, with air temperature increases of the order of 4° to 7 °C over this century (ACIA, 2005; IPCC, 2007). As a result of its high capacity to store heat, the ocean will not warm quite as much as the land. Precipitation and runoff will increase in northern Europe and the Arctic (IPCC, 2007).

Reductions and increases in seasonal ice coverage and thickness have occurred concurrently with the warm and cool periods (Johannessen et al., 2004; ACIA, 2005). There was a 20% decrease in the summer extent of the Arctic sea ice during the last 30 years of 20th century (Johannessen et al., 1999) that extended into the present century with a historic minimum being recorded in 2007 (Kwok and

Rothrock, 2009). In addition the amount of multi-year ice has significantly declined, and the ice has thinned (Rothrock and Zhang, 2005; Kwok and Rothrock, 2009). A consequent decrease in albedo because of the reduction in sea ice led to increased absorption of solar radiation (heating), thereby adding to the increased rate of warming (ACIA, 2005; Fig. 2). The previous IPCC assessment suggested an ice-free summer in the Arctic by 2100 (Teng et al., 2006) but during the past few years the observed summer sea-ice extent has been declining much more rapidly than these models predictions (Stroeve et al., 2007). Present models indicate that the summer sea-ice will disappear by 2050 or before (Stroeve et al., 2007; Overland and Wang, 2007; Kerr, 2009).

Because of the extensive ice cover, difficult logistics, few inhabitants, and a lack of commercial fisheries in the high Arctic, there are few published studies on the biological consequences of past climate changes in this region (Loeng et al., 2005). However, benthic studies in the Chukchi Sea north of the Bering Sea have shown changes in the dominant species, which are thought to be related to changing hydrographic conditions (Grebmeier et al., 1995). Based on satellite measurements of chlorophyll-a between 1998 and 2007, Arrigo et al. (2008) suggested that primary productivity in the Arctic has increased. They concluded that this was a result of a longer growing season and higher light levels because of the reduction in sea ice. This is consistent with predictions by Loeng et al. (2005), which indicated that the losses in ice algal production associated with the reduction in sea-ice coverage would be more than made up for by increased open ocean plankton production in the ice-free regions (Loeng et al., 2005). This increased primary production, in turn, could lead to increased zooplankton and fisheries production (Bouchard and Fortier, 2008). Because of its impact on light attenuation, sea ice also modifies the vertical migration of zooplankton beneath (Berge et al., 2009); hence the reduction in ice cover could lead to changes in zooplankton behaviour.

Benthic production changes will depend upon the match/mismatch between phytoplankton and zooplankton, which in turn will affect the amount of phytoplankton that sinks to the bottom before being eaten (Loeng et al., 2005). Higher production at lower trophic levels is expected to lead to increased zooplankton and fish production in the Arctic (Loeng et al., 2005). In contrast, ice-dependent species such as

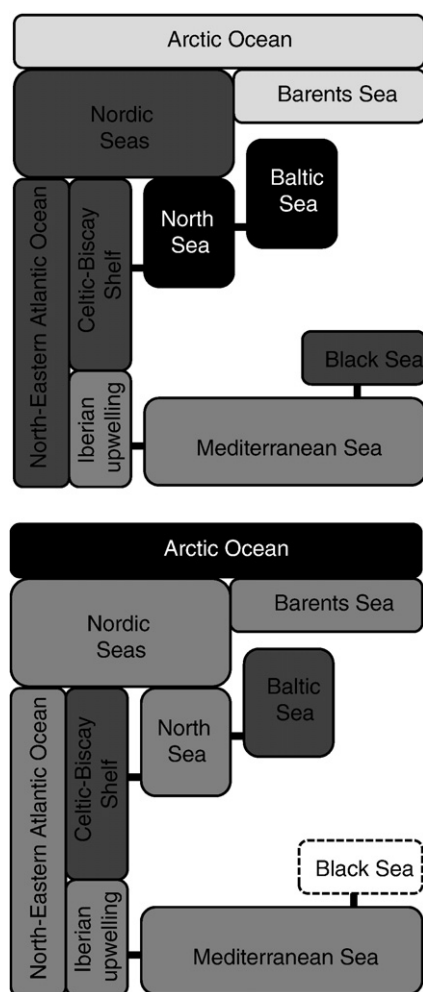


Fig. 2. Observed (top panel) and predicted (bottom panel) changes in SST in European marine systems. Light grey indicates a slow increase (<0.01 °C year⁻¹), medium grey a moderate increase (0.010–0.029 °C year⁻¹), dark grey a fast increase (0.030–0.049 °C year⁻¹), and black a super-fast increase (≥ 0.050 °C year⁻¹). See text and Table 1 for references. No prediction is available for the Black Sea.

polar bears, as well as some seals and several seabird species are likely to decrease in abundance (Kovacs and Lydersen, 2008; Durner et al., 2009; Mallory et al., 2009). Already polar bears are showing some signs of being in poor condition, which is linked to the decline in ice coverage affecting the availability of seals on which to prey (Durner et al., 2009). Distributional shifts in organisms from phytoplankton to marine mammals and seabirds are likely to bring non-indigenous species into the Arctic, adding to a temperature-mediated geographical retraction of native Arctic species and the possibility of some species disappearing altogether (Cheung et al., 2009). Warming in the Arctic and the disappearance of sea ice is facilitating trans-polar movement of plankton from the Pacific to the Atlantic (Reid et al., 2007) and in future is expected to result in increased trans-Arctic transport of biota such as molluscs (Vermeij and Roopnarine, 2008) and the mixing of various species from plankton to marine mammals in these two oceans as well as within the Arctic Ocean (Loeng et al., 2005).

2.2. Barents Sea

The waters in the Barents Sea have undergone similar long-period temperature changes to those in the Arctic and throughout the European Seas (Drinkwater, 2006; Fig. 2). These changes are due to a

combination of atmospheric heating and cooling, and variability in both the volume and temperature of the incoming Atlantic water (Ingvaldsen et al., 2003; Sandø et al., 2010). Associated with warm and cool periods, sea-ice coverage has contracted and expanded, respectively. Although coverage was previously low in the 1930s, it has been near its minimal recorded value in recent years.

From modelling studies, Furevik et al. (2002) suggested that surface ocean temperatures in the Barents Sea are expected to warm by 1° to 2 °C between the mid-1990s and 2080, with winter sea-ice almost disappearing. Atlantic waters will spread farther eastward and northward, and the surface mixed layer depth will increase due to stronger winds (Furevik et al., 2002). In spite of projected increases in precipitation and hence runoff in northern Europe, ocean modelling studies are predicting an increase in salinity in the Atlantic Water inflows, generated by higher evaporation in the tropics (Bethke et al., 2006). Huse and Ellingsen (2008) examined changes in the position of the Polar Front that separates the cold Arctic waters in the northern Barents Sea from the warm Atlantic waters. The frontal position was projected to change little in the western Barents, where it is tied to topographic features, but in the eastern Barents the front will move farther north and east.

Primary production levels have been suggested to be 400% higher in ice-free regions in a warm year compared to when these same areas are ice-covered (Slagstad and Wassmann, 1996). Reduced ice cover has been projected to result in between an 8% (Ellingsen et al., 2008) and 30% (Slagstad and Wassmann, 1996) increase in primary production. This will be due to a combination of higher light levels and longer growing season in areas of decreased ice extent, higher nutrient levels as the Atlantic waters extend farther northward and eastward in the Barents Sea, and faster turn-over times of the phytoplankton due to the higher temperatures. In regions where the seabed or the depth of mixing is <40 m diatom blooms would be favoured, whereas if mixing extended to about 80 m it would be more likely to favour *Phaeocystis* spp. (Loeng et al., 2005). If the surface mixed layer extended beyond about 80 m, it is possible that a low-productive community dominated by nanoflagellates would be favoured. This would imply little transfer of carbon to herbivores and the sediments because the grazers would be largely ciliates (Sakshaug and Walsh, 2000).

During the warm period of the 1920s to 1950s, fish such as cod, haddock and herring expanded northward and eastward (Drinkwater, 2006). Similar responses have occurred during the recent warm period (Drinkwater, 2009). In addition, large numbers of blue whiting have extended northward as far as the south-western Barents Sea (Dolgov et al., 2010). Blue mussels (*Mytilus edulis*) have appeared in Svalbard after a 1000 year absence (Berge et al., 2005). An expansion of Atlantic-associated benthic species has occurred while Arctic species declined (Berge et al., 2005). Under the projected warming in the Barents Sea, Atlantic Water species of fish and benthos are expected to extend farther east and north (Stenevik and Sundby, 2007). The higher primary production is expected to produce increased catches of cod, haddock and other species (ACIA, 2005). Improved growth rates together with expected increased recruitment will lead to higher fish yields for commercial species such as cod, although this will depend to a large degree upon fishing intensity (Drinkwater, 2005).

More fish will spawn farther north, as observed for cod, and new spawning sites are likely to be established (Sundby and Nakken, 2008). Herring and blue whiting will likely spread farther eastward and salmon abundance is likely to increase in Russian waters as observed during previous warm periods (Lajus et al., 2005) and also extend to northern Spitzbergen. Capelin will follow the Polar Front farther to the northeast to feed and are expected to continue to spawn off northern Norway, but also establish new spawning sites along the northern Russian coast as well as off Novaja Zemlja (Huse and Ellingsen, 2008). The distribution shifts of fish will bring more of the major commercial species (such as cod and haddock) into Russian waters, which may require renegotiation of present fisheries treaties

between Norway and Russia (Stenevik and Sundby, 2007). However, due to a projected increase in overall fish production, landings are expected to increase for both countries.

2.3. Nordic Seas

In response to atmospheric heating and advection of warm water into the region during the late 20th Century, rapid warming of the waters occurred in all three basins: the Greenland, Norwegian and Iceland Seas (Fig. 2). In the Norwegian Sea this was a result of higher heat transport by the Atlantic Waters, whereas in the Greenland Sea it was because of warmer waters flowing out of the Arctic. Since the mid-1980s there has been a steady increase of more than 0.5 °C for the waters between 1200 m and 2000 m, and even the deepest water has shown a small temperature increase (Østerhus and Gammelsrød, 1999). Sea surface temperatures are expected to increase by a further 1° to 2 °C during the 21st Century (Furevik et al., 2002; Fig. 2).

In warm periods during the last century, Norwegian spring spawning herring migrated northwards to areas off north-eastern Iceland (Vilhjálmsón, 1997). As the Arctic Front shifted south-eastward during the colder 1960s, the herring moved farther eastward and then to the southwest of Spitzbergen. When the population declined to low levels because of a combination of deteriorating climate conditions and heavy fishing pressure, the remaining individuals stayed near the Norwegian coast to both feed and spawn (Vilhjálmsón, 1997; Toresen and Østvedt, 2000). In the 1990s, as temperatures warmed and the population increased, they began migrating back towards Iceland to feed (Loeng et al., 2005). The projected warming under climate change is expected to produce good environmental conditions for herring.

Capelin, the major prey of adult cod off Iceland, have moved closer to Greenland in recent years (personal communication, O. Pálsson, Institute of Marine Research, Reykjavik, Iceland). The cause of this distributional shift is unknown. Similar changes in geographic location were observed during the early 20th century warming period, but to different locations.

In recent years, warm conditions due to the increased influx of Atlantic waters off northern Iceland have led to higher recruitment of fish (Jónsson and Vladimarsson, 2005). This may be due to a shorter growth period during the vulnerable larval stages, increased food because of higher primary and secondary production (Astthorsson and Vilhjálmsón, 2002) or a combination of both. Phytoplankton blooms may last longer due to reduced stratification and higher nutrient concentrations in water of Atlantic origins.

The biological responses to the predicted physical changes are expected to include a slight increase in primary production north of Iceland due to the greater presence of Atlantic waters, and off East Greenland as a response to enhanced light levels due to the absence of sea-ice. It is expected that the abundance of Arctic zooplankton species will decrease, while Atlantic species should increase. Growth and condition of cod, haddock and capelin should improve and these species will likely move or spread further northward eventually regularly occupying the waters around the island of Jan Mayen. Atlantic herring should again begin to overwinter to the east of Iceland and move north-westwards with the Arctic Front. More southern species are likely to invade the Nordic Seas, with some becoming frequent visitors. These invasions may lead to an increase of biodiversity within the fish communities of the Nordic Seas.

2.4. Northeast Atlantic Ocean

Over the period 1965–2004, the North Atlantic was a region of net heat accumulation (Palmer et al., 2007; Fig. 2). However, the pattern of changes was asymmetric across the basin with cooling in the northwest and warming in the northeast, until recently when the northwest region also showed strong warming (Hughes et al., 2008). Pronounced decadal variability is evident as a result of wind stress changes with a deepening of the North Atlantic subtropical gyre from

1981 to 2005 following an earlier period from 1959 to 1981 when the thermocline became shallower (Leadbetter et al., 2007). The southerly outflow through the Faroe Shetland Channel decreased by 20% in the last 50 years (Hansen et al., 2001) and the northward flow of surface waters has reduced since the 1970s (Häkkinen and Rhines, 2004). The ocean is freshening both at the surface and at depth (Curry et al., 2003; González-Pola et al., 2005) and has undergone a period of rapid warming (Levitus et al., 2000). Associated changes have taken place in the circulation and in the formation of deep water, both in the Nordic Seas and in the Labrador Sea. All these conditions together are likely to reduce the Thermohaline Circulation and could eventually lead to a cooling of Europe's climate, possibly in a matter of decades. Modelling studies to date, however, suggest that this is unlikely to happen in the next 100 years and that the current trend of warming is likely to continue with increases of 2 °C or more over this time frame.

The observed increase in sea temperatures, especially in winter months since the mid-1980s, has had a marked effect on the plankton and higher trophic levels. Over the last 40 years, warmer water groups of plankton to the west of the British Isles have moved north by c.1000 km (Beaugrand et al., 2002). Mid-water to surface-water fish have shown similar northerly extensions in their ranges (Quero et al., 1998; Brander et al., 2003). Both total biomass and growing season of phytoplankton have increased since the mid 1980s (Reid, 2005). Atlantic salmon have shown dramatic declines in their returns to home waters that appear to be linked to climatic variability (Beaugrand and Reid, 2003). Most other exploited fish species in the region, including deepwater species, have also undergone large reductions in stock size, an impact that is believed to be due, in large measure, to overfishing, but which may also include an environmental component. Recently, it was found that the sensitivity of certain ecosystems to temperature change depends on whether they are close to the critical thermal boundary of 9–10 °C, which represents a large-scale ecological threshold in the North Atlantic Ocean (Beaugrand et al., 2008) and coincides with the transitional region between the Atlantic Polar and the Atlantic Westerly Winds biome (Longhurst, 1998).

The oceans play a crucial role in the carbon cycle as the main (non-geological) reservoir for carbon (32,000 Pg estimated as stored in the deep ocean). Perhaps the greatest impact of climate change will be on the carbon pumps, these routes by which CO₂ in the atmosphere is drawn down to a reservoir in the deep ocean (Reid et al., 2009). The four 'carbon pumps' (Solubility, Biological, Continental Shelf and Carbonate Counter) sequester CO₂ at the surface of the ocean and transfer it, largely as dissolved inorganic carbon to the deep ocean reservoir thus reducing levels in the atmosphere. Since the beginning of the industrial revolution release of CO₂ to the atmosphere, primarily from burning fossil fuel and land use change, has resulted in a net flux from the atmosphere to the ocean on top of an already active oceanic carbon cycle (Takahashi et al., 2009). There is an uneven distribution of anthropogenically sourced CO₂ in the ocean, and the North Atlantic, given its size (15% of the global ocean), has taken up more than its share (23%) (Sabine et al., 2004). This ocean is an especially important sink for CO₂ because of its favourable Revelle factor, productivity, alkalinity and because of the deep mixing that occurs in this region. Against this background, there is evidence in the North Atlantic that the rate of CO₂ uptake may already be reducing (Schuster and Watson, 2007).

The 'Solubility' pump operates most efficiently at low temperatures where the uptake of CO₂ as dissolved inorganic carbon (DIC) is much higher due to increased solubility and at high latitudes where water draws down. This process only occurs in the sub-polar seas of the North Atlantic (not in the North Pacific) and in the Southern Ocean (Reid et al., 2009). It is estimated that the Solubility pump has become less efficient in the northern North Atlantic (Sabine et al., 2004) due to the warmer temperatures that have occurred over the last decade or more; a view that is supported by the observed reduction in the density of the deep water found in the Norwegian Sea.

The 'Continental Shelf' pump is a form of the biological pump and is likely to be important and strongly affected by some of the major ecological changes that have occurred in European shelf seas in recent decades. The 'Carbonate Counter' pump involves the production and dissolution of calcium carbonate and its sedimentation to the ocean bottom. It should be noted that when calcium carbonate is formed by organisms it releases CO₂ to the atmosphere. Changes in the pH of the ocean may lead to the dissolution of calcium carbonate sediments in parts of the ocean (The Royal Society, 2005).

Phytoplankton account for approximately 50% of the total photosynthesis on Earth, and provide food for higher trophic levels. The 'biological pump' transfers CO₂ fixed by photosynthesis to the deep ocean primarily as dead organisms (including organic and carbonate skeletal and faecal material). Although only a small proportion of the total annual production of the plankton ends up in the deep ocean, there is strong evidence to suggest that this pump contributes importantly to the different levels of atmospheric CO₂ found between glacial and interglacial periods (Raven and Falkowski, 1999), possibly due to changes in relative fluxes of fast-sinking diatoms versus small and rapidly ingested calcareous plankton (Harrison, 2000; Treguer and Pondaven, 2000).

If present trends in anthropogenic CO₂ continue to rise for the next several hundred years, this may have severe implications for many species of CaCO₃ shell-forming organisms, such as calcifying phytoplankton and foraminifers but also coral reefs and deep-water reef ecosystems (The Royal Society, 2005; Guinotte et al., 2006). Their existence is threatened by the increasing acidity of the ocean caused by higher levels of atmospheric CO₂.

Plankton can act as ballast for the export of carbon to the deep ocean with the organisms that have mineralised skeletal parts playing an important role. Siliceous diatoms and calcareous foraminifera, coccolithophores and molluscan pteropods and cephalopods are important ballast organisms. Changing production, composition and seasonal timing of the plankton, due to rising temperatures and increasing acidity, may affect the efficiency of the downward transfer of organic material. Any reduction in this drawdown will further accelerate the increase in CO₂ and global warming (The Royal Society, 2005).

2.5. North Sea

In the North Sea, temperature has been an important driver of trophodynamics for nearly 50 years (Kirby and Beaugrand, 2009). Within this time, two climatic periods that were characterised by a wide-scale and rather sudden change in plankton, benthos and fish populations stand out as exceptional (e.g. Weijerman et al., 2005; Kirby and Beaugrand, 2009). The first change occurred in the late 1970s, and was distinguished by a reduced inflow of Atlantic water and cold-boreal conditions (Reid and Edwards, 2001; Reid and Edwards, 2001). During the most recent change in the late 1980s, oceanic inflow increased markedly, as did sea surface temperature (Reid et al., 2001; Beaugrand, 2004; Fig. 2). This warm temperate period has continued to the present day. In the future, air temperatures over the North Sea are expected to increase by 2 °C to 3.5 °C by the 2080s (Fig. 2), with high summer temperatures becoming more frequent and very cold winters becoming increasingly rare (e.g. Hulme et al., 2002; van den Hurk et al., 2006).

Seasonal changes in the timing of biological events for different functional groups in the plankton as a response to warming are leading to a mismatch in the timing between phytoplankton and zooplankton, between zooplankton and fish, between bivalve larvae and shrimp, and between fish and seabirds (e.g. Beaugrand and Reid, 2003; Edwards and Richardson, 2004; Philippart et al., 2003; Wiltshire and Manley, 2004). In the past 40 years, the warming of the North Sea has affected cod recruitment via changes at the base of the food web (Beaugrand et al., 2003).

Northerly range extensions or changes in the geographical distribution of plankton and fish populations are associated with the above changes and have been related to regional climate warming (Beaugrand et al., 2003; Brander et al., 2003; Perry et al., 2005; Dulvy et al., 2008). The range of warmer water species of plankton, for example, has extended northward by 1000 km in only 40 years, and colder species have retreated out of the North Sea (Beaugrand et al., 2003). Sardines and anchovies have moved northward in the North Sea and red mullet and bass extended their ranges north to western Norway (Brander et al., 2003). On average, North Sea fish have also shifted to deeper waters. For example, a demersal fish assemblage consisting of 28 North Sea species has deepened significantly at a rate of ~3.6 m decade⁻¹ between 1980 and 2004 (Dulvy et al., 2008). Many warm-water rocky shore snails and barnacles formerly absent or just extending into the North Sea from the warmer waters of the British west coast have spread south from the tip of Scotland along the North Sea coast of the UK (Mieszkowska et al., 2005; Mieszkowska, Hawkins and Burrows, personal observations).

In summary, the change in temperature in the late 1980s established a new ecosystem dynamic regime by modifying the strength and direction of many trophic interactions and favouring jellyfish, decapods and echinoderms (Kirby and Beaugrand, 2009; Gibbons and Richardson, 2009). This strongly suggests that the North Sea ecosystem is vulnerable to variation in climatic conditions in general, and to anomalies in temperature and hydrodynamics in particular. Several processes within the North Sea food web appear to be triggered by temperature, and further increases in temperature may continue to disrupt the connectedness between species potentially leading to changes in community structures and possibly local extinctions. For many marine species, including commercially caught fish, large and co-varying fluctuations in recruit densities mainly determine the year-to-year variation in the size of the adult stocks. If the annual sea surface temperature increases further, efforts to maintain previous fishery yields from reduced stocks (due to northward movement and lowered recruitment levels) have the potential to significantly impact fisheries and have dramatic effects on the ecosystem (Brander, 2007).

2.6. Baltic Sea

The Baltic Sea is a semi-enclosed sea with a total area of 415,000 km² including the Kattegat. The catchment area is four times larger and inhabited by approximately 85 million people. Climate variability in the last 150 years overlaps with human activity in the drainage basin and the coastal zone leading to considerable change in the biogeochemistry of the enclosed sea. The Baltic Sea is characterised by a closed basin circulation (Voss et al., 2005) and by strong horizontal gradients both in salinity and in ecosystem variables. The salinity gradient is responsible for the low biodiversity of the Baltic Sea with marine species in the entrance to the North Sea decreasing eastwards to be replaced by freshwater species in the inner reaches. Beside the Arctic Seas (ACIA, 2005), the Baltic Sea is the only regional sea for which a climate assessment report has been compiled (BACC, 2008).

The inter-annual and inter-decadal variability of the Baltic Sea is influenced by the climate variability of the Northern Hemisphere and Major Baltic Inflows (MBI) of water with high salinity from the North Atlantic passing through the North Sea into the deeper parts of the Baltic Sea (Matthäus and Frank, 1992; Elken and Matthäus, 2008). Ice extent and ice thickness in the Baltic Sea are significantly related to the large-scale atmospheric circulation patterns in the Arctic and North Atlantic described by the Arctic Oscillation (AO) index and the North Atlantic Oscillation (NAO) index (Loewe and Koslowski, 1996; Koslowski and Glaser, 1999; Omstedt and Chen, 2001). While there are many similarities between the AO and NAO, the AO appears to better describe the dynamics of the sea-ice conditions in the Baltic than the NAO (Jevrejeva et al., 2003). Atmospheric forcing influences the general circulation and the sea level. Approximately 85% of the variability in sea level anomalies can be explained by the NAO and 10% by the so-called

'Vb storm track' (Heyen et al., 1996); this is the only persistent cyclone pathway in Europe which may cause extreme precipitation and huge flooding of central European rivers during summer time (Mudelsee et al., 2004). However, a linear correlation analysis indicates that the NAO accounts for about 10% of the general volume exchange of the Baltic Sea with the North Sea, whereas the regional Baltic Sea Index has a much better explanatory power (Lehmann et al., 2002).

A long-term analysis of 100 years of hydrographic data with a focus on the freshwater budget (Winsor et al., 2001, 2003) indicates that freshwater supply (river runoff plus precipitation minus evaporation) to the Baltic Sea shows large variations on time scales up to several decades. Analysis of a cumulative Baltic winter index shows that, during the last 350 years, six regime shifts have occurred (Hagen and Feistel, 2005). Since the Baltic Sea has decadal climate modes on the order of 30–60 years, it is thus difficult to clearly define climatic "trends" or "regime shifts" on shorter time scales (Omstedt et al., 2004).

The Baltic Sea ecosystem appeared to be strongly influenced by the interplay of non-periodic shifts from freshwater to marine conditions and back during the late quaternary period (Andr n, 2004). This in turn resulted in changes in the relative composition of marine and freshwater species, shifts from cold water to warm water species and back, changes between oxygen-rich and oxygen-poor conditions in the deep basins, and the occasional intrusion of non-indigenous species (Dippner et al., 2008 and references therein).

Observations show that the Baltic Sea has experienced significant warming over the last century with associated changes including increased winter runoff, a shorter sea-ice season and reduced ice thickness. A continued rise in temperature under greenhouse forcing is projected by climate models for the coming century. The additional warming may amount to 3 to 5 °C in the atmosphere (model and emissions-dependent) and 2 to 4 °C in sea surface temperature in the Baltic by the end of the 21st century (Graham et al., 2008; Fig. 2). As a result, the extent of sea-ice is expected to reduce by 50% to 80%.

Increasing temperatures prevent spring convection and therefore the redistribution of nutrients with major consequences for net primary production and the structure of marine communities (Wasmund et al., 1998). Higher temperatures during winter will result in increased metabolic rates for bacteria and a shift in species composition from cold to warm water species, whereas higher temperature in summer may enhance cyanobacteria blooms (Janssen et al., 2004). In addition, higher temperatures may lead to an increase in the carrying capacity for sprat stocks and probably alter food web structure (M llmann et al., 2005).

Future projections of precipitation vary depending both on emissions levels and differences between climate models. Seasonally, winters are projected to become wetter in most areas and summers drier in the south for many scenarios. Increasing precipitation during winter will cause higher river runoff and reduced salinity. Lowered salinity is thought to have a major influence on the distribution, growth and reproduction of the Baltic Sea fauna. It will cause osmotic stress for phyto- and zooplankton and result in a shift in species composition from marine to freshwater species. Such a shift influences food quality and therefore the growth rate and fat content of fish (M llmann et al., 2003). Decreasing salinity in combination with hypoxia will cause poor survival conditions for cod eggs (MacKenzie et al., 2000). However, model projections with transient forcing from emission scenarios A1B and B1 (Hollweg et al., 2008) for the period 1960–2100 indicate that decreasing reduction in salinity will cause an increase in mixed layer depth and hence a decrease in the extent of the suboxic area (Neumann, 2010).

For the marine ecosystem of the Baltic Sea, assessment of the component of change associated specifically with climate is complicated by the presence of other anthropogenic stressors, particularly eutrophication and fishing. Expected changes in the amount, distribution and seasonality of runoff may have additional detrimental effects on the problem of eutrophication. An increase in precipitation will result in higher nutrient or DOM input by rivers and enhanced eutrophication in near coastal areas with higher phytoplankton and benthic biomass

(Dippner and Ikauniece, 2001). A combination of effects from climate change scenarios with changes in primary emissions of nitrogen has been investigated by H gg et al. (2010) for 105 catchments surrounding the Baltic Sea. Human protein consumption is projected to increase up to 2100 resulting in a 16% to 39% increase in mean total nitrogen flux. Combining these results with four climate change scenarios showed a considerable range (from 3% to 72%) of possible increases in total nitrogen flux. If the demand for animal protein increases as projected, it may be a major obstacle to fulfilling the environmental goals of the Baltic Sea Action Plan (HELCOM, 2007).

Studies of the combined effects of climate change and fisheries have also been carried out, including their influence on zooplankton dynamics and biological regime shifts (M llmann et al., 2008, 2009) and consequences for the sustainable resource management of fisheries (Lindgren et al., 2009, 2010). M llmann et al. (2008) have demonstrated a linkage between climate-induced zooplankton and fish regime changes and how overfishing may amplify the climate-induced changes at both trophic levels. These regime shifts have important management implications, as they can cause significant losses of ecological and economic resources. Because Baltic cod is close to its physiological tolerance level, such changes in amplitude and duration of extreme climate events (e.g. the frequency and duration of MBLs) are likely to have greater consequences than changes in mean values (Brander, 2007). The application of a complex model hierarchy showed that an ecosystem-based approach provides quantitative stock forecasts for Baltic cod and suggests adaptive management actions to mitigate negative effects on future fisheries production under climate change (Lindgren et al., 2009, 2010).

2.7. Celtic-Biscay shelf

The pattern of change in sea surface temperature for this region reflects that found throughout much of the North Atlantic since the 19th century. Following a warm period in the 1880s, sea surface temperatures cooled until the early 20th century before increasing from around 1920 and remaining warm until the 1960s. A cooler period followed the extremely cold winter of 1962/1963 and continued well into the 1980s, followed by accelerated warming (Southward et al., 2005; Fig. 2). Similar changes have been seen in the Bay of Biscay (Planque et al., 2003; Blanchard and Vandermeersch, 2005), the Irish Sea (Evans et al., 2003) and the Eastern English Channel (Woehrling et al., 2005). Over the next 100 years in this region, sea water temperatures are predicted to increase between 1.5° and 5 °C (Fig. 2).

During the warming in the 1930s, the herring fishery in the English Channel collapsed, and herrings were largely replaced by pilchards (sardines) (see Southward, 1980; Hawkins et al., 2003, for reviews). Historical research has shown that such switches were commonplace and have been occurring at least since the 13th Century during alternating cold or warm periods (Southward et al., 1988). In the 1960s there was a switch back to colder conditions and the planktonic communities returned to their previous colder water characteristics. Pilchards declined again. Herring did not recover – perhaps because at that time (1970s) stocks were at historically low levels in the eastern English Channel and North Sea due to overfishing, and recolonisation occurred at much lower rates (Hawkins et al., 2003). Sardines are now abundant again and macrozooplankton such as the warmer water chaetognath *Sagitta setosa* and other southern species predominate (Southward et al., 1995, 2005; Hawkins et al., 2003).

Since the late 1980s, warm temperate zooplankton species which just reached the region in the 1960s started to spread northwards towards the west coast of France, Britain and Ireland (Beaugrand et al., 2002). In the 1960s and 1970s, warm water species of barnacles (*Chthamalus* spp.) were partly replaced by the cold water barnacle *Semibalanus balanoides* (Southward, 1967; Southward et al., 1995, 2005). At present, however, warm water barnacles now exceed the levels found on the rocky shores in the 1950s. This is particularly the

case in the eastern English Channel and on the north west of Scotland where several species of barnacles, gastropods and limpets have penetrated far beyond their previous northern limits (Mieszowska et al., 2005, 2007; Helmuth et al., 2006; Hawkins et al., 2008, 2009). Some boundaries have been breached by several species, but for *Chthamalis* barnacles, there has been little progress eastwards in the English Channel due to hydrographical barriers coupled with lack of suitable habitats and Allee effects (Herbert et al., 2007, 2009).

Forecast models of intertidal assemblages suggest that northern species (such as the barnacle *Semibalanus balanoides*) will go extinct in much of the southwest of England and probably also in northwest France in the next 20 to 30 years (Svensson et al., 2005; Poloczanska et al., 2008). Some species, such as the kelp *Alaria esculenta*, were badly impacted by the last warm period of the 1950s and seem to have regressed further in recent years (Mieszowska et al., 2005). The implications for shifts in geographic distribution of intertidal species have been discussed in relation to changes in ecosystem functioning: primary producers such as canopy forming fucooids are thought likely to become less dominant in the British Isles and be replaced by barnacle- and grazer-dominated communities as is currently found in Portugal (Hawkins et al., 2008, 2009).

By 2025, even under low emission scenarios, the fish, benthic and rocky shore assemblages might resemble those currently found to the south in the Iberian Peninsula (Hiscock et al., 2004; Genner et al., 2004, 2010; Genner, Hawkins, Sims, unpublished projections). The possibility still remains of rapid cooling at some stage should the Thermohaline Circulation be much reduced leading to a weaker Gulf Stream. Should this occur, then rapid re-adjustment to northern assemblages is likely, as occurred after the last extremely cold winter of 1962–1963 (Genner et al., 2004, 2009; Sims et al., unpublished).

2.8. Iberian upwelling margin

The Iberian upwelling area is characterised by a narrow shelf crossed by deep canyons (e.g. Avilés canyon); the river runoff to the area is low with the only important rivers in the west Iberian Peninsula: Duero, Tajo and Guadalquivir, all with large estuaries. The whole area is located in a region with weak circulation patterns that change seasonally. The most characteristic signature is seasonal upwelling that fertilises the coastal waters in summer. This process enhances primary productivity in the area, increasing fisheries productivity as well as that of the extensive mussel and other aquaculture operations. The upwelling also influences the presence of boreal species in the northwest corner of the Peninsula (Southward et al., 1995; Lima et al., 2006; Wethey and Woodin, 2008). The region coincides with the Iberian coastal Large Marine Ecosystem (LME), considered by Sherman et al. (2009) as a rapidly warming area in which fisheries are decreasing.

During the last century, the northern part of the Iberian Coastal margin (located within the southern part of the Bay of Biscay) experienced two cold periods, around 1910 and 1970, and warm temperate periods around 1870 and 1960 (Planque et al., 2003). In the last few decades, rapid warming in surface temperatures ($0.055\text{ }^{\circ}\text{C year}^{-1}$ over 30 years) has occurred in all the oceanic areas but not in the coastal regions of this area (Koutsikopoulos et al., 1998; Llope et al., 2006; Gómez-Gesteira et al., 2008; Fig. 2). In very near coast locations along northern Spain, the long-term trend in temperature could even be negative (Borja et al., 2002; Goikoetxea et al., 2009).

A decreasing salinity trend in the surface and sub-surface waters towards the southern Bay of Biscay was observed in the last fifteen years (González-Pola et al., 2005). An averaged sea level rise of 2.12 to 2.91 mm year^{-1} in the last 50 years was detected in the northwest Iberian Peninsula (Marcos et al., 2005), with a 6.5 mm year^{-1} rise between 1991 and 2001. A decreasing trend in the upwelling index and the seasonality of upwelling off northern Spain has also been detected during the last thirty years (Llope et al., 2006; Pérez et al., 2010), which is in contrast to previous findings by Bakun (1990).

A reduction in primary productivity was detected on shelf areas of the northwest Iberian Peninsula (Llope et al., 2007; Castro et al., 2009), whereas no changes were observed in coastal waters. Diatom abundance also reduced and dinoflagellates increased off the southern Galician coast (Pérez et al., 2010). A rapid increase (1993–1994) in the abundance of the rare warm temperate copepod *Temora stylifera* occurred in the Bay of Biscay, which correlated with the decreasing abundance of the coastal species *Temora longicornis* (Valdés et al., 2007). Several other organisms of subtropical origin have also been detected during recent years (Guerra et al., 2002).

There have been similar changes in the species abundance and diversity of intertidal communities (Sánchez et al., 2005), with northward displacement of species of southern origin (Lima et al., 2006, 2007a, 2007b), biomass decreases of some seaweeds of boreo-atlantic origin, like *Fucus serratus*, *Laminaria ochroleuca* and *Chondrus crispus* (Anadón et al., 2009a, 2009b; C. Fernández, personal observation), an increase in the biomass of some warm temperate species (e.g. *Bifurcaria bifurcata*, and displacements on the distribution boundaries of species described by Anadón and Niell (1980) on the north Spanish coast, all of which suggest a rapid response to climatic changes in the past decade or so.

There have also been changes in exploited fish populations such as pilchard, sardine, anchovy, mackerel and horse mackerel, but it is difficult to differentiate between climate and fishing effects (Anadón et al., 2009a, 2009b). Many climate-related changes such as alterations in migratory routes and spawning areas, however, are associated with fluctuations in the NAO index (Borja et al., 2002). New exploitable fish species have appeared in commercial fisheries, like *Scomber japonicus* or *Balistes capriuscus*, with increased landings in recent years (Bañón, 2009). The area supports intense fisheries and aquaculture via traditional mussel rafts and modern intensive fish and mollusc farming, and the observed increase of harmful algal blooms could affect these commercial activities (Fraga and Bakun, 1993; Álvarez-Salgado et al., 2009). Changes in primary productivity that are related to upwelling intensity and seasonality affect growth of shellfish during the summer period (Álvarez-Salgado et al., 2009) and the quality (Blanton et al., 1987) of mussels. An increase in parasites of subtropical origin, such as shellfish parasites of the genus *Perkinsus*, is a possible threat to the extensive mollusc farming along the Spanish coasts (Labarta, personal observation).

Depending on the latitude, changes in sea surface temperature range are predicted to be between 1.4 and 2.4 $^{\circ}\text{C}$ from 1960–1990 to 2070–2100 (scenario CM2.1, SRESA1B (run1) 720 ppm stabilisation experiment (SRES A1B) output for IPCC AR4 and US CCSP as made by the Geophysical Fluid Dynamic Laboratory, NOAA, Princeton, NJ, USA). These changes as well as the observed and predicted changes in circulation and stratification (González-Taboada and Anadón, submitted) could influence the retention–dispersion mechanism of larval stages of fish and shellfish with unknown consequences for species recruitment. Based on temperature limits of their distribution and global climate models on future sea surface temperature, the distribution of seaweed and invertebrate fauna is expected to move along the northwest Iberian and Atlantic French coasts during the first half of the 21st century (Alcock, 2003; Lima et al., 2007a, 2007b). Changes in storminess have been predicted over the next decades that may affect beaches and sediment in coastal areas (Losada et al., 2004; Anadón et al., 2009a, 2009b). The projected sea level rise could also seriously impact on coastal and wetland ecosystems (Cendrero et al., 2005).

2.9. Mediterranean Sea

The enclosed Mediterranean basin is a miniature ocean (*sensu* Lejeune et al., 2010) where the effects of climate change are likely to be more apparent earlier than in other more open oceans (Coll et al., 2010). The Mediterranean Sea appears to be warming as a whole (Bethoux et al., 1990; Astraldi et al., 1995; Walther et al., 2002; Fig. 2). In recent decades, a rapid warming of surface water masses has been

observed (0.04 ± 0.01 °C year⁻¹ over 24 years) (Diaz-Almela et al., 2007). Using an Atmosphere–Ocean Regional Climate Model (AORCM), Somot et al. (2008) predict an increase in annually averaged SST of 2.6 °C between 1961–1990 and 2070–2099.

Marine biodiversity of the Mediterranean is changing in response (Francour et al., 1994). In the Adriatic Sea, warming temperatures and salinity variations intensified after 1988 (Russo et al., 2002) along with evidence of progressive acidification and decrease of the carbonate ion concentration (Luchetta et al., 2010). In combination with other climate changes (increases in storm frequency and rainfall, and changes in wind speed and direction), this had an impact on water properties (e.g. salinity, mixing, and altered turbidity) (Russo et al., 2002). The richness of microclimates in the Mediterranean, ranging from climate conditions similar to those of the North Sea in the Adriatic to almost tropical conditions in the Eastern Mediterranean, makes any prediction at large spatial scales difficult.

Climate change is influencing the boundaries of biogeographic regions with some warm water species extending their ranges and colonising new regions where they were previously absent. Observed changes involve both indigenous species subjected to a process named ‘meridionalization’ and non-indigenous species, subjected to a process defined as ‘tropicalization’ (Boero et al., 2008). Such changes are causing a progressive ‘homogenization’ of the marine biota within the Mediterranean Basin. These processes have been reported for both highly mobile fish species and for sedentary organisms and benthic macroalgae (Bianchi, 2007). The western Mediterranean has experienced outbreaks of jellyfish (Moliner et al., 2005). The warming of Ligurian Sea waters has favoured the penetration of warm-water species (Bianchi and Morri, 1994; Puce et al., 2009), and, in the Adriatic, an increase in fish and zooplankton species (Dulcic and Grbec, 2000; Kamburska and Fonda-Umani, 2006). In the Mediterranean Sea, the euphausiid *Meganyctiphanes norvegica* is at the southern limit of its ecological tolerance, and constitutes the only known food resource of the fin whales (*Balaenoptera physalus*). If the present climate change alters the distribution or abundance of the prey species, this will probably have important consequences for large cetaceans (Gambaiani et al., 2009). The rise of seawater temperatures may be partly responsible for changes in the range of some species, creating maritime corridors linking this region to other warm seas and regions. The invasion of non-indigenous species has, however, resulted in the dislocation of other species (CIESM, 2002) and cascade effects on food webs (Moliner et al., 2008).

Current changes are favouring the increasing introduction of non-indigenous species (Galil, 2007; Occhipinti-Ambrogi, 2007). Most of the non-indigenous species in the Mediterranean are thermophilic originating in the tropical Indo-Pacific (Lessepsian migrations – Galil, 1993). The list of exotic animals and plants that have invaded the Mediterranean, and particularly the Eastern Mediterranean, is continuously increasing, and today more than 600 species have been reported (Coll et al., 2010; Costello et al., 2010). In littoral habitats, not only single allochthonous species but also entire alien assemblages of Red Sea origin (e.g., the “*Tetraclita* community”) have established (Ben Souissi et al., 2007). Even though the introduction of new species is increasing the list of species living in the Mediterranean Sea, the consequences in term of ecosystem functioning are still largely unknown (Boero and Bonsdorf, 2007). Increasing temperatures in the last 30 years are altering the flowering of the seagrass *Posidonia oceanica*, which is an endemic species of the Mediterranean Sea (Diaz-Almela et al., 2007), with a higher intensity of flowering apparently related to the increasing temperatures. The changes are causing a progressive disappearance from the surface layer of stenothermic species, which may have moved to deeper layers. Some phytoplankton species such as the genus *Ceratium* have also been affected with changes to their phenology (Tunin-Ley et al., 2009). Seawater temperature rise is also increasing the risk of extinction of cold-water species in the Northern Adriatic Sea, one of the most vulnerable Mediterranean areas to climate change. For

example, the macroalgae *Fucus virsoides*, a glacial relict and endemic species, is at risk because there is nowhere for it to retreat (Boero et al., 2008).

Temperature anomalies, even of short duration, have had large effects on Mediterranean faunal diversity. In the western Mediterranean, a positive thermal anomaly during summer combined with an increase in the warm mixed layer down to a depth of 40 m (Romano et al., 2000) resulted in an extensive mortality of 28 invertebrate species (Cerrano et al., 2000; Perez et al., 2000; Garrabou et al., 2009). In the Adriatic Sea, the abnormally low surface temperatures, from 9 °C to freezing, in the winter of 2001 led to mass mortalities of sardines (*Sardinella aurita*) (Guidetti et al., 2002), with consequent alteration of the foodwebs. A similar displacement of this species to northern areas in the Spanish Mediterranean related to positive anomalies in temperature was also detected (Sabatés et al., 2006). A decline in temperature of about 0.4 °C in the eastern Mediterranean between 1992 and 1994 caused an increase by ca. 50% of nematode diversity coupled with a decrease in the functional (trophic) diversity. The subsequent warming of deep-sea temperature, which occurred from 1994 to 1998 and is continuing in the last decade, was coupled with a significant decrease of nematode diversity (Danovaro et al., 2001). Such changes are associated with an increasing direct anthropogenic impact on deep-sea biodiversity (Danovaro et al., 2010).

Climate change in the Mediterranean also favours epidemiological outbreaks, as most pathogens are temperature sensitive. Mass mortalities of the gorgonian *Paramunicea clavata*, scleractinian corals, zoanths, and sponges observed in 1999 in the Ligurian Sea were promoted by a temperature shift (Cerrano et al., 2000), which favoured the development of pathogenic agents (such as *Vibrio* spp.; Bally and Garrabou, 2007; Vezzulli et al., 2010). The coral-bleaching bacterium *Vibrio shiloi* was involved in the mass mortalities of the coral *Oculina patagonica* (Kushmaro et al., 1998). A recent study has reported that the spread of large amorphous aggregates (mucilage) in the Mediterranean Sea is linked to climate-driven sea surface warming. The mucilage, including several microbial species that are apparently lacking in surrounding seawaters, can act as a controlling factor of microbial diversity across wide oceanic regions and could have the potential to act as a carrier of specific microorganisms. In particular the mucilage contains several species of pathogenic bacteria and viruses and could contribute to their spread in different regions (Danovaro et al., 2009). Morbilliviruses that cause seal epidemics have also been identified in Mediterranean monk seals (van de Bildt et al., 1999).

2.10. Black sea

During the 1980s, the upper layer of the water column of the Black Sea cooled significantly in response to large increases in the NAO index (Oguz et al., 2006). The strength of winter cooling was marked by a more than 1.5 °C drop in the winter mean sea surface temperature during the first half of the 1980s. During more recent years, however, the temperature of the surface waters of the Black Sea rapidly increased (Belkin, 2009; Fig. 2). At present, there is no projection available on how climate change may affect this region. Although data show well-defined oscillations during the past 100 years, there is no reason to expect that these oscillations will not continue in the future. However, these oscillations may have been superimposed on a more well-defined general trend of warming. The Black Sea region is influenced by several teleconnection patterns, making future predictions more challenging than for areas that are mainly modulated by, for example, the NAO alone.

The Black Sea ecosystem has undergone some major changes during the last 50 years. However, the intense eutrophication together with over-exploitation of pelagic fish stocks were mainly responsible for the shift from the classical phytoplankton–zooplankton–fish food chain to an alternative pathway dominated by gelatinous and opportunistic species including the invasive, non-native comb jelly *Mnemiopsis leidyi*

Table 2

Summary of scenarios of effects of climate change on species composition of marine communities in European seas.

General trends	System-specific expectations
Increase in temperature	Higher in northern than in southern systems Higher in enclosed than in open systems
Impacts on ecosystems	Stronger for enclosed than for open systems
Northward movements	Higher in northern than in southern systems Stronger for open than for enclosed systems
Shifts in species composition	From northern to southern species (open systems) From ice-bound to aquatic species (northern systems) From marine to freshwater species (Baltic Sea) From endemic to congeneric species (enclosed systems)

(Prodanov et al., 1997; Shiganova, 1998; Gucu, 2002; Daskalov, 2002; Oguz et al., 2006).

The Black Sea has been impacted by the adverse effects of climatic warming after the mid-1990s, which led to low nutrient levels in the surface layer and a subsequent decrease in phytoplankton abundance. As a consequence all higher trophic levels were less productive due to limited resource availability. The decline of *Mnemiopsis*, however, helped small pelagic fish to recover. Another gelatinous carnivore *Beroe ovata*, preying mainly on *Mnemiopsis*, was introduced into the Black Sea with ballast waters in 1998. Predation on *Mnemiopsis* by *Beroe* was rapidly reflected by a two-to-three fold increase in mesozooplankton biomass, ichthyoplankton biomass, and fish stocks (Kideys, 2002; Shiganova et al., 2003).

Due to the absence of local climate projections for this area and the ongoing strong influence of other external factors besides climate change such as eutrophication, overfishing and the introduction of non-indigenous species, no predictions on the future development of the ecosystem can be made at this time.

3. Synoptic trends and system-specific expectations

3.1. Increase in temperatures

Recent research, including the examination of ice cores and growth rings of ancient trees, shows that the Northern Hemisphere has been warmer since the 1980s than at any other time during the last 2000 years (Mann and Jones, 2003; Moberg et al., 2005). The observed and predicted increases in temperature under climate change are generally higher in northern than in southern European seas and in enclosed than in open systems (Fig. 2; Tables 1 and 2),

although local deviations from this pattern occur, such as the sharp temperature increase in the Adriatic Sea (Russo et al., 2002). For the most northern seas, such as the Arctic and the Barents Sea, the most obvious temperature-related change is the decline in sea-ice cover. Both areas are predicted to be ice-free during summer within the next 40–50 years. The disappearance of the ice may increase local production of the sea (Loeng et al., 2005). The reduction of the formerly ice-covered area is expected to result in a decline, and possible extirpation of the animals that depend on this habitat, such as ringed seals and polar bears. At a larger scale, the reduction of the ice-covered areas may lead to an increase in heat absorption and changes in convection and water mass formation, possibly affecting temperature and ocean currents globally.

3.2. Northward movements

Many marine species are moving northwards. The rate and direction of this migration, however, differs for the diverse seas and species. Enclosed seas, such as the Baltic, the Mediterranean and the Black Sea, have only small and primarily east–west orientated corridors which may restrict northward migration in these areas (Figs. 3 and 4). The distribution range of boreal-Atlantic species in the northwest of the Iberian Peninsula has been reduced due to a reduction in upwelling. Further warming will presumably drive the marine species with a preference for cooler waters up to the northern coastlines of these areas, followed by extinction if they are not able to adapt to the new circumstances in time (Table 2). In the North Sea and English Channel, invasion of warm-water species can be from the south or the west, originating in the more oceanic waters off the western coasts of Britain, Ireland and France, which have relatively high winter temperatures. Noticeably, the enclosed seas appear to have undergone far more dramatic changes than the more open seas during recent decades. Relatively small changes in the frequency of inflow (Baltic Sea) or in temperature (Eastern Mediterranean and Black Sea) have had a strong effect on large parts of the ecosystem. This implies that although the temperature increase is predicted to be relatively small in the more southern waters, the effect of climate change is still likely to be quite large in these waters.

For most open seas, there is evidence of species moving northwards and/or northern species being replaced by more southern ones. Such changes not only affect the local ecosystems, but also the international fishing industry when commercial species such as cod (Mieszkowska et al., 2009) are involved. It must be noted, however, that a climate-induced decline in fish stocks lead to over-fishing if harvesting yields are not changed accordingly. Under such

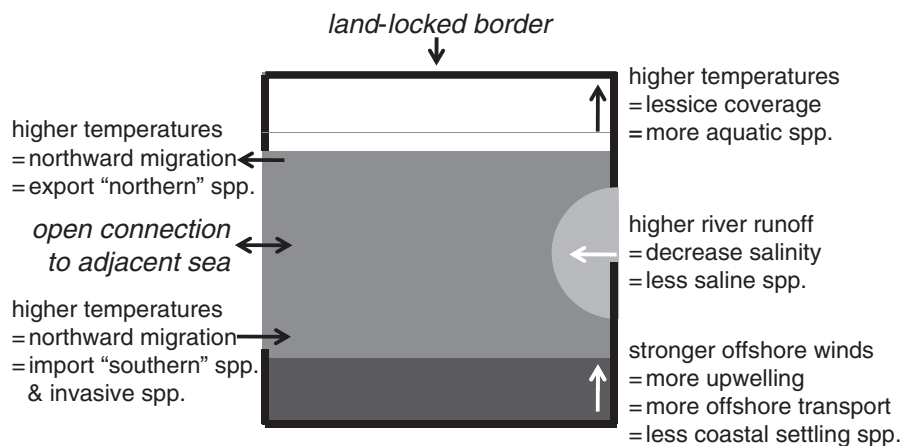


Fig. 3. Hypothetical overview of possible effects of climate change on species composition of marine communities in a semi-enclosed sea (thick black lines indicate enclosure by land) which is ice-covered in winter, experiences seasonal upwelling, is influenced by freshwater from a main river, and is connected to other seas in the south and in the north.

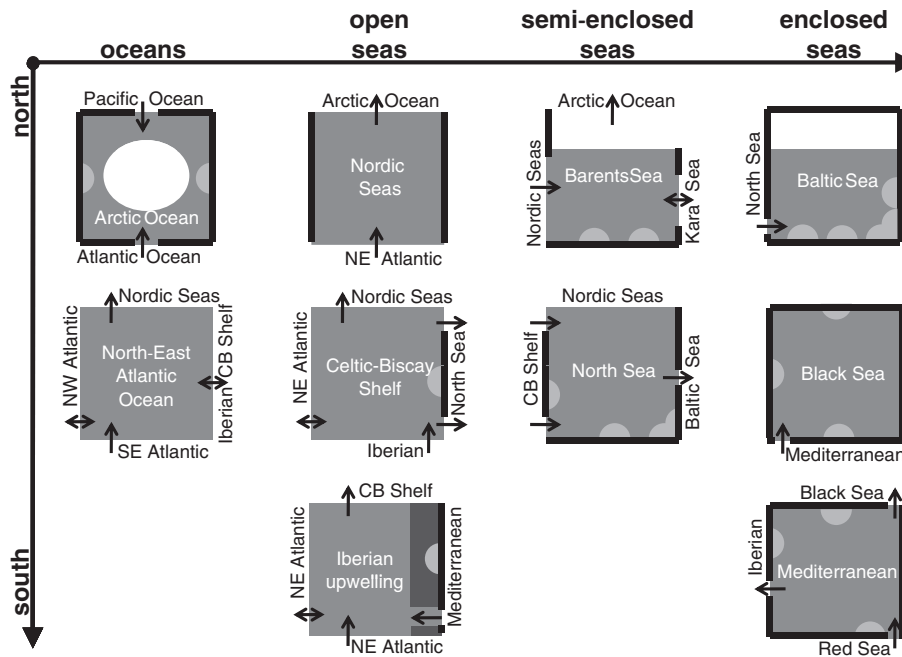


Fig. 4. Schematic overview of hypothesised effects of climate change on changes in species composition of marine communities in European oceans (Arctic Ocean, and Northeast Atlantic Ocean) and seas (Barents Sea, Nordic Seas, North Sea, Baltic Sea, Celtic-Biscay Shelf, Iberian upwelling margin, Mediterranean Sea, and Black Sea).

circumstances, it is impossible to distinguish between the effects of climate change and over-fishing. Even in the more open seas, however, species did not always move northwards if prey were not available. Both in the Barents Sea and in the North Sea, marine mammals were observed to migrate southwards when their prey stocks collapsed. Such changes indicate that detailed knowledge of the physiology, bioenergetics and behaviour of species is needed to adequately predict the impact of climate change on the distribution of marine organisms and marine food webs.

3.3. Shifts in species composition

It is expected that within open systems there will generally be northward movement, from polar to more temperate species in the more northern seas such as the Arctic, Barents Sea and the Nordic Seas and from temperate to more subtropical species in the southern seas such as the Iberian upwelling margin (Table 2; Figs. 4 and 5). For seas that are highly influenced by river runoff, such as the Baltic Sea, an increase in freshwater due to enhanced rainfall will lead to a shift from marine to more brackish and even freshwater species. If enclosed systems such as the Baltic, Mediterranean and the Black Sea lose their endemic species, their niches might be filled by species originating from adjacent waters and from other sources such as ballast water and Lesepian transfers via the Suez Canal (Table 2).

3.4. Coastal waters

European seas border more than 68,000 km of coastline, harbouring internationally important wetlands, and major cities and ports. The combination of an accelerating sea level rise and a possible increase in the frequency and intensity of storms as predicted for most European seas will severely increase the risk of flooding and subsequent loss of these areas (Airoldi et al., 2005; Burcharth et al., 2007). Further extension, raising and reinforcement of artificial coast defences may protect populated areas, but are bound to result in loss of sedimentary coastal marine habitats with consequences for living marine resources including aquaculture (Airoldi et al., 2005; Martin

et al., 2005; Anderson et al., 2005). Such artificial coastlines may act as stepping stones for species advancing with climate change (Helmuth et al., 2006; Hawkins et al., 2009) and provide habitat for jellyfish polyps, contributing to the increases in jellyfish (Richardson et al., 2009). Many marine organisms, including economically important fish, spend part of their life in the relatively sheltered areas along the coast. Loss of these areas may affect these animals in that specific part of their life cycle. In addition, changes in the strength and seasonality of upwelling in areas along the coast could influence the retention-dispersal mechanisms of (juvenile) fish and shellfish between coastal waters and open sea with unknown consequences for species' recruitment.

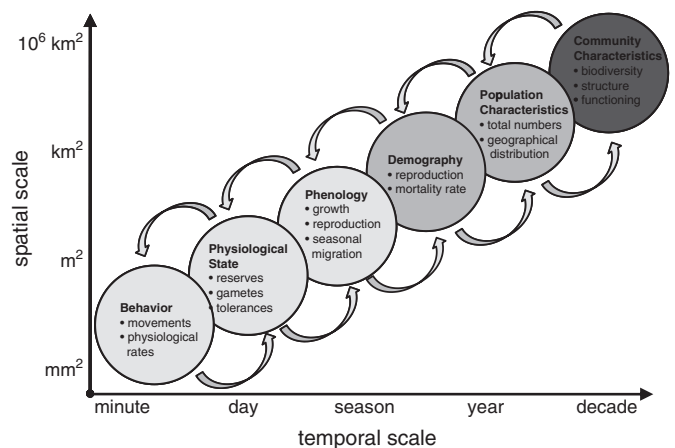


Fig. 5. Expected impacts of climate variability on marine species (light grey), populations (medium grey) and communities (dark grey) at various temporal and spatial scales. See Table 3 for examples of potential indicators for these impacts. Note that the actual values on the scales will depend on the length of the life cycle and the mobility of the species under consideration (e.g., short-lived sedimentary species generally operate at smaller scales than long-lived migratory species).

3.5. Impacts on ecosystems

In general, further increase in temperature are expected to be higher in northern than in southern systems, and to be higher in enclosed than in open seas and oceans. Subsequent northward movements of marine species are, generally, expected to be lower in semi-enclosed and closed systems than in open systems, in particular in those systems that are closed at the northern side such as the Baltic Sea, the Black Sea and Mediterranean (Figs. 3 and 4). Open systems may, therefore, experience a shift from northern to more southern species. The species composition of closed systems such as the Baltic Sea, Black Sea and Mediterranean is expected to suffer from the loss of endemic species with the invasion of non-indigenous species. In European systems that are (partly) ice covered during winter, higher temperatures are expected to result in a shift from ice-bound to aquatic species. In the Baltic Sea, an increase in precipitation and a decrease in the frequency of major Baltic inflows from the North Sea will result in a shift from marine to more brackish and freshwater species.

4. Future research needs

4.1. Gaps in knowledge

From the preceding analysis of climate change impacts on European marine and coastal waters, a number of research needs can be identified. These include the identification and further analysis of historical data to describe past ocean climate and ecosystem development, and a better understanding of biogeochemical fluxes, food web dynamics and ecosystem functioning, including feedback mechanisms, under current predictions of climate change. To predict future CO₂ concentrations in the atmosphere there is a need for a much improved understanding of the way that the biological pump varies both geographically and temporally and the effects on the pump of changes in temperature, ocean circulation and ocean chemistry (e.g. acidification due to increased CO₂). Increased understanding will enable the development of improved regional climate models and predictive ecosystem models.

There is a need to examine how climate change will affect structural and functional biodiversity, how the structure (e.g. species composition, food web length, and size distribution) and functioning (e.g. biomass, production and decomposition processes, and predator–prey interactions) of marine ecosystems will change under current predictions of climate change and how changes in the chemical composition of elements in the ocean will influence food web dynamics. Research is needed on the possible consequences of climate change for the nature and strength of the interactions between the various trophic levels of the system, including the possibility of cascading effects. Predicting when and under what conditions climate-induced ecosystem regime shifts will occur, and if such changes will be reversible (and if so what are the recovery dynamics) are also needed. Such research should be performed at the proper scale in time and space at the various levels, spanning individual short-term small-scale behavioural responses to long-term large-scale changes in biodiversity and the functioning of marine communities (Fig. 5).

Marine ecosystems appear to be already affected by climate change in most European seas (Philippart et al., 2007). Although all ecosystems have been influenced by many other factors, such as eutrophication and over-fishing, every region examined has shown at least some changes that were most likely the direct or indirect result of recent climate change. Although there can be no certainty regarding the precise nature and rate of future climate change, even the most conservative scenarios expect further changes to the marine environment. For future planning and development of adaptation strategies, it is necessary to better understand and predict the ultimate consequences of climate change in relation to concurrent

effects of other stressors such as changes in nutrient loads, invasion of non-indigenous species and exploitation of marine living resources. The investigation of combined effects and the possible consequences for human health are a great challenge for the future.

4.2. Indicators of climate change

Specific indicators can be used to monitor trends and detect sudden changes in environmental conditions which are considered to be the result of climate variability (short time scale) and/or climate change (long time scale). An indicator (e.g. sea temperature or length of growing season) is defined here as a variable or measure that reveals some key element of a system. Its value and long-term trend indicates the present state relative to a baseline and thus measures dynamics of the system. None of the indicators, however, is likely to be influenced by climate change alone. Groups of indicators will, therefore, be needed to conclusively demonstrate if and how climate change is affecting marine systems.

Indicators should be simple (easy to understand and to measure), reliable (conceptually and methodologically well founded) and affordable. Indicators based on ongoing long-term monitoring programmes and projects can take advantage of tested protocols for routine collection of data, historical data for estimation of reference values and build up confidence in interpretation. If long-term monitoring protocols have to be adapted for new indicators, however, some conflict may arise between consistency and improvement.

Physical indicators of potential climate change consist of ocean forcing functions (atmospheric and hydrological) as well as sea-ice and oceanographic properties (see Table 3), whilst biological indicators consist of five groups of indicators related to organisms (behavioural aspects, state of the body, and phenology of biological events), to populations (recruitment, mortality, numbers and geographical distribution) and to community structure (biodiversity, structure and functioning) (see Table 3). These represent a minimum suite of indicators needed to address climate change issues and determine possible causes of ecosystem changes.

4.3. Recommendations

With regard to future monitoring, indicators and future research needs, we recommend that the following is required:

1. Enhanced evaluation of the impact of climate change on the European marine and coastal environment; this will require a concerted effort to gather, store and analyse previously and presently collected marine environmental data (e.g. common open access database and annual pan-European reporting based on national contributions);
2. Identification of the nature and rate of consequences of climate change in European marine and coastal waters; this will require the maintenance and expansion where necessary of existing long-term monitoring programmes that are pan-European in scope, and standardisation where possible between single site surveys combined with new technologies to improve the detail of information available as well as increase their spatial and temporal resolution;
3. Prediction of the consequences of climate change for our marine environment; this will require the development and measurement of parameters (e.g. indicators) which are indicative of the underlying mechanisms of climate-induced changes;
4. Prediction of the response and feedback of marine environments and ecosystems to climate change; this will require the improvement of regional climate models and the development of biophysical models;
5. Prediction of the impact of climate change on the distribution of marine organisms and on marine food webs; this will require the inclusion of knowledge on the physiology, bioenergetics and behaviour of species in biophysical and ecosystem models.

Table 3
Overview of potential indicators for impacts of climate variability on European marine systems.

Indicator	Example/observation	Reference
<i>Physical indicators</i>		
Atmosphere		
Pressure systems	North Atlantic Oscillation AO	Lamb and Pepler, 1987; Hurrell, 1995; Hurrell and Deser, 2009 Thompson and Wallace, 1998; Thompson et al., 2000
Weather	Air temperature Precipitation	Chen and Hellström, 1999; Rummukainen et al., 2004 Mudelsee et al., 2004; Rummukainen et al., 2004
Freshwater and ice		
River runoff	Annual sums Seasonal variations Peaks and droughts	Bergström and Carlsson, 1994; Winsor et al., 2001, 2003 Bergström and Carlsson, 1994; Winsor et al., 2001, 2003 Graham, 2004; Graham et al., 2007
Sea ice	Total coverage Thickness Age (single year/multiyear)	Loewe and Koslowski, 1996; Koslowski and Glaser, 1999; Omstedt and Chen, 2001; Jevrejeva et al., 2003 Loewe and Koslowski, 1996; Koslowski and Glaser, 1999 Johannessen et al., 2004
Oceanography		
States	Temperature Salinity Mixed layer depth Stratification Heat content Sea-level elevations	Meier, 2006; Belkin, 2009 Zorita and Laine, 2000; Meier and Kauker, 2003; Neumann, 2010 Neumann, 2010 Neumann, 2010 Omstedt et al., 2000 Heyen et al., 1996; Meier, 2006
Rates	Volume transports channels and straits Upwelling indices	Lehmann et al., 2002 Lehmann et al., 2002
<i>Biological indicators</i>		
Behaviour		
Feeding rates	Bivalve filtration rates	Oliver et al., 2008
Prey selection	Diet seabirds	Abraham and Sydeman, 2006
Vertical migration	Vertical excursions sea stars	Garza and Robles, 2010
Physiological state		
Tolerances	Thermal tolerance whelks Hypoxia tolerance fish Wing length birds	Somero, 2010 Portner, 2010 Yom-Tov et al., 2006
Body size	Body mass polar bears	Derocher, 2005
Cognitive abilities	Decline kittiwakes	Kitaysky et al., 2005
Phenology		
Rapid growth	Phytoplankton spring bloom	Lassen et al., 2010
Reproduction	Flowering seagrass First egg dates seabirds Spring migration shrimps Spring migration birds Sea mammals	Duarte et al., 1999 Wanless et al., 2009 Philippart et al., 2003 Hüppop and Hüppop, 2003 Meier et al., 2004
Population dynamics		
Reproduction	Mean age at maturity seals Reproductive volume Year-class strength fish Condition seabird chicks Weather-induced starvation	Krafft et al., 2006 MacKenzie et al., 2000 Dippner and Ottersen, 2001 Kitaysky et al., 2005 Tranquilla et al., 2010
Mortality		
Population characteristics		
Size	CPR colour index Satellite-derived chlorophyll-a Spawning stock biomass fish Range extension Abundance-weighted centres Connectivity Non-indigenous species Depth bottom-dwelling fishes	Beaugrand, 2009 Boyce et al., 2010 Drinkwater, 2009 Hawkins et al., 2008 Rivadeneira et al., 2010 Berge et al., 2005 Galil, 2007 Dulvy et al., 2008
Geographical range		
Depth distribution		
Community characteristics		
Species composition	Colder/warmer affinities Diatoms/flagellates Species richness Atlantic fish Plankton composition	Southward et al., 1988 Wasmund and Uhlig, 2003 Hofstede et al., 2010 Beaugrand et al., 2010
Biodiversity		
Functioning	Biological carbon pump	Beaugrand et al., 2010

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