Sub-chapter 2.1.2

Climate change induces bottom-up changes in the food webs of the Mediterranean Sea

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At the global scale, one of the main effects of climate change on marine ecosystems is changing the rate and patterns of primary production (Brown et al. 2010). In the Mediterranean Sea, although there is no consensus and no clear trends have emerged, several studies expect that, by increasing the vertical stability of the water column and by decreasing nutrient replenishment, seawater warming will cause changes in phytoplankton bloom phenology, biomass and community structure (Goffart et al. 2002, Bosc et al. 2004, Tunin-Ley et al. 2009). What has been clearly demonstrated is that seawater warming will lead to a shift in dominant species towards smaller species (picophytoplankton and nanoflagellates) and a decrease in diatoms (The MerMex Group 2011). Moreover, acidification in the Mediterranean Sea will strengthen the expected impacts, with an expected decrease in the biomass of calcifying organisms such as coccolithophorids, which are important plankton primary producers (Dias et al. 2010, The MerMex Group 2011). Primary and secondary production (i.e. the production of phytoplankton and zooplankton, respectively) play a key role in biogeochemical cycles, as well as in the structure and functioning of food webs and in global productivity of marine ecosystems. Through bottom-up or wasp-waist trophic controls (Cury et al. 2003), changes at the base of the food webs may transfer from low to high trophic levels, with potential impacts on the production of living resources and fisheries. Moreover, since the Mediterranean is a semi-enclosed sea, expected impacts of climate change on phytoplankton communities and their dynamics could affect ecosystems much more rapidly than in other oceanic regions (Lejeusne et al. 2010, Siokou-Frangou et al. 2010). In this chapter, we describe how climate change could affect the functioning of marine systems, and more specifically, the production of living resources by bottom-up control. We use a few typical recent examples to show how the strength of the bottom-up control and the base of the food web in the Mediterranean Sea could be affected by several hydrological changes and how these changes could affect food web dynamics, catch potential, and conservation of the marine biodiversity in the future.

Changes in primary and secondary production affect food web dynamics and recruitment

At the global scale, under the IPCC SRES (Intergovernmental Panel on Climate Change Special Report on Emission Scenarios) A2 scenario, and based on the output of four global coupled carbon cycle-climate models, Steinacher et al. (2010) suggest that global mean primary production may decrease by 2% to 20% by 2100 relative to preindustrial conditions. In the Mediterranean Sea, by increasing the strength of the vertical stratification, warming could affect the turbulent nutrient supply to the photic layer and hence could reduce primary production (Marbà et al. 2015), as well as reduce the relative contribution of larger cells (The MerMex Group 2011). There are still many uncertainties on the level of impact of sea warming and of acidification on primary production in the basin, but it is clear that physical-chemical changes will affect the magnitude, timing and composition of phytoplankton blooms, with associated changes in the seasonal distribution of zooplankton (see sub-chapter 2.1.1 for more details).

It is now recognized that primary production is critical to maintain biodiversity and support fishery catches in the world's oceans (Brown et al. 2010). Indeed, more than 90% of ocean productivity is ensured by phytoplankton, which is then transferred throughout the food webs by grazing and predation and lost through metabolism (Lindeman 1942, Gascuel et al. 2008). Few studies have tried to forecast potential changes in primary and secondary production and the ensuing impacts on food webs and on the functioning of Mediterranean ecosystems. Many uncertainties remain concerning the magnitude of the expected climate-induced changes. Nevertheless, based on studies of other ecosystems in the world, it is possible to extrapolate the consequences of changes in primary production in this region. For instance, Chassot et al. (2010) showed that phytoplankton primary production influences global fisheries production at the scale of Large Marine Ecosystems (LME). This assumption was confirmed by Blanchard et al. (2012), who showed that, in 11 large regional shelf seas, potential marine fisheries production is primarily determined by available primary production. Similarly, using an ecosystem model, Brown et al. (2010) demonstrated that changes in primary production affect fisheries catch and value and have major implications for the conservation of marine biodiversity. Finally, at local, regional and global scales, several authors have established that fluctuations in fishery yields are linked to fluctuations in phytoplankton, zooplankton and benthic communities (e.g. Darnaude et al. 2004, Edwards & Richardson 2004, Cheung et al. 2010, Barange et al. 2014).

In the Mediterranean Sea, previous observations already suggested that a reduction in primary production linked to an increase of sea surface temperature could have negative impacts on fisheries catch and could exacerbate current trends of overfishing. This hypothesis was confirmed by Cheung et al. (2011) whose models predict that if phytoplankton communities shift towards smaller size cells, energy transfer from primary production to higher trophic levels may decline in the future, with an associated reduction in catch potential (see sub-chapter 2.1.4). Moreover, a decrease in primary production could be detrimental for the conservation of taxa of interest and for overall biodiversity in a context of global change, with potential synergies with overfishing, habitat degradation and biological invasions.

In marine ecosystems, environmental conditions play an important role in fish recruitment (i.e. the number of fish that survive from the early larval stage to reach the recruitment stage that can be targeted by fisheries). As fish larvae are very vulnerable to starvation, their survival strongly depends on prey availability, meaning the mean size of prey, their seasonal timing and abundance (Beaugrand et al. 2003) are crucial. The match-mismatch hypothesis (Cushing 1990) emphasizes that the production of first feeding larvae must match the production of planktonic food. Thus, by affecting primary and secondary production and timing, climate change may disrupt the distribution and phenology of fish larvae, affect recruitment and production of fish stocks, with indirect effects on food web structures and ecosystem-level changes (Edwards & Richardson 2004, Brander 2010). In the Mediterranean Sea, projected changes in primary and secondary productions suggest that trophic mismatches between fish pre-recruits and their prey could increase in the future, with negative consequences for recruitment success, sustainable fisheries and conservation of biodiversity (Lejeusne et al. 2010, Stergiou et al. 2015).

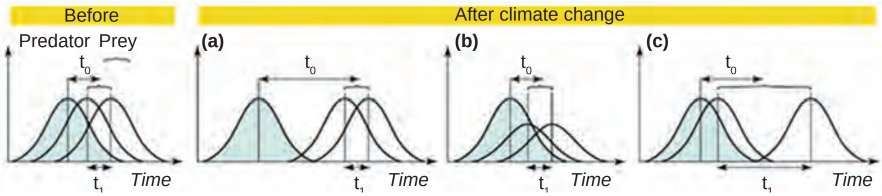

Figure 1
Match-mismatch hypothesis and three possible effects of climate change:
(a) Change in the timing of prey peak production; (b) Change in the level of prey abundance;
(c) Change in the amplitude of year-to-year variations in prey timing in regions where inter-annual variability in temperature is expected to increase. t_0 is the degree of time mismatch,
t_1 is the inter-annual variability in the timing of prey population.
From Cury et al. (2008).

In addition to impacts on plankton production and timing, climate change can also lead to changes in the composition of species that form the base of marine food webs. In the Mediterranean Sea, the increase in water temperature has already modified jellyfish population dynamics (Coll et al. 2010). For several decades, the extent and intensity of jellyfish outbreaks have increased, in particular outbreaks of *Pelagia noctiluca*, a planktonic predator of fish larvae and of their zooplankton prey (Licandro et al. 2010). In the western Mediterranean, the increasing frequency of these outbreaks can be explained by the alteration of the trophic structure of ecosystems due to overfishing and/or eutrophication on the one hand, and by sea warming and changes in surface hydrography on the other (Licandro et al. 2010, Canepa et al. 2014). As already shown in the Black Sea, outbreaks can affect fisheries by bottom-up and top-down controls on fish larvae survival (Daskalov et al. 2007). In fact, jellyfish can affect fish recruitment negatively and as they can be venomous, outbreaks can also be detrimental to aquaculture and have strong ecological and socio-economic impacts. Considering the current IPCC projections, Licandro et al. (2010) suggested that outbreaks of *P.noctiluca*, along with other jellyfish species, may become more frequent in the Mediterranean basin and extend over a longer period of the year than previously, causing alteration of the pelagic food web and thereby reducing fishery production. For instance, in the northwestern Mediterranean Sea, Molinero et al. (2005) found that the increase in jellyfish outbreaks during the 1980s was largely favored by high positive temperature anomalies. They highlighted the trophic cascade that took place during the mid-late 1980s, with the high abundance of jellyfish and a marked drop in the abundance of copepods. However, the variability of copepods has direct implications for pelagic fish populations and for the biological pump of carbon into the deep ocean (Ohman & Hirche 2001, Calbet 2008). Thus, the Mediterranean pelagic ecosystem could shift towards an alternative state with less organic matter exported and prone to the risk of high trophic level predators (exploited by fisheries) being replaced by jellyfish (Gros 2011).

Another consequence of climate change in the Mediterranean Sea, which, at first sight, has less impact on fisheries, is the increase in the mucilage phenomenon. Indeed, surface water warming and the associated increase in water column stability can favor the coalescence of marine snow (i.e. small amorphous aggregates with colloidal properties) into marine mucilage (Danovaro et al. 2009). Danovaro et al. (2009) have shown that the majority of mucilage spreading is linked to climate-driven sea surface warming. The occurrence of mucilage events is increasing and spreading to several regions beyond the Adriatic Sea. Mucilage can act as a controlling factor for microbial diversity and could act as a carrier of specific microorganisms, thereby increasing the spread of pathogenic bacteria (Danovaro et al. 2009). According to these authors, if the mucilage phenomenon continues to increase in frequency and duration and to extend its range in the region, the increased frequency and extension of some marine diseases may have consequences for human health; "a warmer world would be a sicker world" (Harvell et al. 2009). Mucilage, in turn, can induce hypoxic phenomena, extensive anoxia and may reduce the provision of ecosystem services and ecosystem resilience. Indeed, hypoxia or anoxia events can cause the suffocation of benthic and epibenthic organisms on the sea bottom, which, in turn, could result in severe fishery and sanitary problems (Danovaro et al. 2005). Moreover, because of mucilage's properties, the phenomena may clog fishing nets causing serious socio-economic damage for fisheries (Rinaldi et al. 1995).

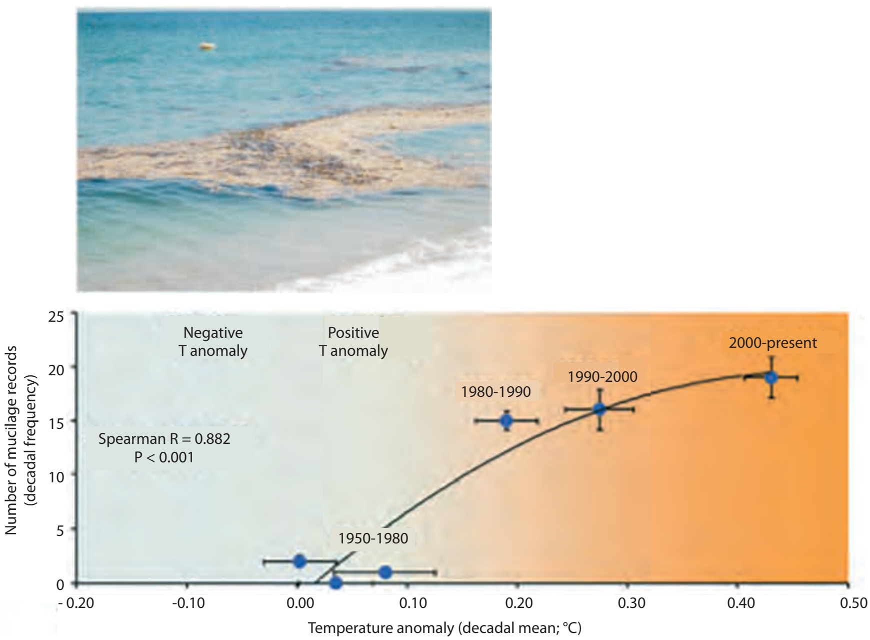

Figure 2
Relationships between mucilage occurrence in the Mediterranean Sea and climate change (as magnitude of the thermal anomalies) on a decadal basis. Photo of mucilage in surface off-shore waters. Adapted from Danovaro et al. (2009).

Climate change drives commercial fish production

Because of their short life span, their nutrition relying on short plankton-based food chains and their recruitment controlled by the environment, pelagic fish stocks are excellent sentinel species for analysis of the effects of climate change on ecosystems (Checkley et al. 2009). This is not surprising, given that these species have a very high growth and population turnover rate, making them more susceptible to changes in the environment. For example, in the western Mediterranean, a significant relationship was found between round sardinella (*Sardinella aurita*) landings and temperature anomalies (Sabates et al. 2006). Indeed, a gradual northward increase in the abundance of this warm water species was observed along the Mediterranean Iberian coast. Consequently, an overall increase in landings of round sardinella has been observed over the last 30 years (around 35 000 t), while landings remained below 5000 t year^{-1} until the early 1980s. This increase is linked to the successful reproduction of the species, marked by an increase in larval abundance, in the northwestern Mediterranean. At the same time and in the same area, landings of two other pelagic species, sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), have declined in recent decades. Sprat (*Sprattus sprattus*), a cold water small pelagic species, has virtually disappeared from commercial catches of the northwestern Mediterranean (Sabates et al. 2006). Using a 3-D full life cycle population model at the Mediterranean Sea LME (large marine ecosystem) scale, under the SRES IPCC A1B scenario, Stergiou et al. (2015) determined that the anchovy biomass would decrease significantly (by around -28 %) in 2080-2100 compared to 1980-2000. This prediction is linked to a decrease in zooplankton biomass and rising temperatures that affect fish metabolic rates (i.e. an increase in maintenance cost). In their study, sea warming was shown to affect net fish somatic growth and to indirectly affect egg production, which is weight dependent. Moreover, with warmer temperatures, fish early life stages could be subject to higher starvation mortalities due to the increased energy required to meet maintenance costs (Stergiou et al. 2015). As a result, anchovy stock biomass is predicted to decrease by 33% in the Adriatic sub-area, by 18% in the north Aegean sub-area and by 15% in the Catalan Sea/Gulf of Lions sub-area.

In the northwestern Mediterranean, numerous changes in environmental conditions such as riverine input or wind mixing can explain fluctuations in the productivity of small pelagic fish (Lloret et al. 2004). For instance, a significant relationship between monthly landings of anchovy and freshwater inputs of the Ebre River during the spawning season of anchovy has been found (Lloret et al. 2004). For sardine, monthly landings were positively correlated with wind mixing during its spawning season (Lloret et al. 2004). Thus, in a context in which climate change is expected to increase variance in rainfall regimes, with increased frequency of droughts paralleled by unusual amounts of rainfall and floods, increasing temperature and changing wind mixing, pelagic fish stocks in the Mediterranean are likely to be strongly impacted (Lloret et al. 2001). In the northwestern Mediterranean, in contrast to anchovy, sardine abundance was found to be negatively correlated with sea surface temperature, and the warming trend may have contributed both to the decrease in sardine abundance and to the extension of the distribution area of the round sardinella (Palomera et al. 2007, Rijnsdorp et al. 2010). In addition to climate change impacts, fluctuations in small pelagic populations have also been shown to be associated with interdecadal variability of climate indices, such as the well-known Atlantic Multidecadal Oscillation (AMO) and the more local Western Mediterranean Oscillation (WeMO) indices (Martín et al. 2012, Alheit et al. 2014).

Pelagic fish are essential trophic compartments of marine ecosystems due to their high biomass at intermediate levels of the food web, and therefore their key role in the transfer of organic matter from lower to higher trophic levels (Cury et al. 2000, Palomera et al. 2007). Hence, variability in small pelagic fish due to climate change or other anthropogenic disturbances will modify both the structure and functioning of ecosystems (Cury et al. 2000). Pelagic stocks are not the only stocks to be impacted by changes in river discharge. Salen-Picard et al. (2002) showed that the Rhone river flow in the Gulf of Lion also influenced abundances of *Solea solea* by causing pulses of organic matter that are followed by peaks of polychaetes density. Indeed, a positive correlation was found between the mean annual commercial landings of *S. solea*, with a time lag of five years, in two fishing harbors close to the Rhone delta (Salen-Picard et al. 2002). The authors of the study concluded that fluctuations in sole fishery yield in the Gulf of Lion can be influenced by climate, as the Rhone river flow is related to the North Atlantic Oscillation, which drives precipitation over Western Europe. In fact, a decrease in run-off into the Mediterranean Sea could reduce the productivity of sole and other demersal fish in this region (Salen-Picard et al. 2002, Darnaude et al. 2004). By coupling a hydrodynamic model to the food web model Ecopath with Ecosim, Libralato & Solidoro (2009) showed that changes in river run-off are the major environmental driver of ecosystem dynamics in coastal areas in the Adriatic, especially the Lagoon of Venice.

To summarize, many uncertainties remain on future change in primary production and more data are needed to carefully assess possible impacts on marine biodiversity and on fisheries production. With this synthesis, we highlight a possible change in the strength of the bottom-up control in the Mediterranean ecosystems. Small pelagics are influenced by a plethora of factors, each of which can be altered by climate change, so that they can have additive, synergistic or antagonistic effects on small pelagics. Climate change is expected to reduce primary production rates at basin scale, to alter the phenology of phytoplankton and zooplankton blooms and to cause shifts in community structures. All these changes will have dramatic impacts on the structure and functioning of ecosystems, and especially on food web dynamics. For fisheries, the change in primary production will likely result in a reduction of catches and/or an exacerbation of the effects of overfishing. Finally, by affecting rainfall regimes, and therefore river outflows, climate change could affect the overall food web and fishery production on the continental shelf.

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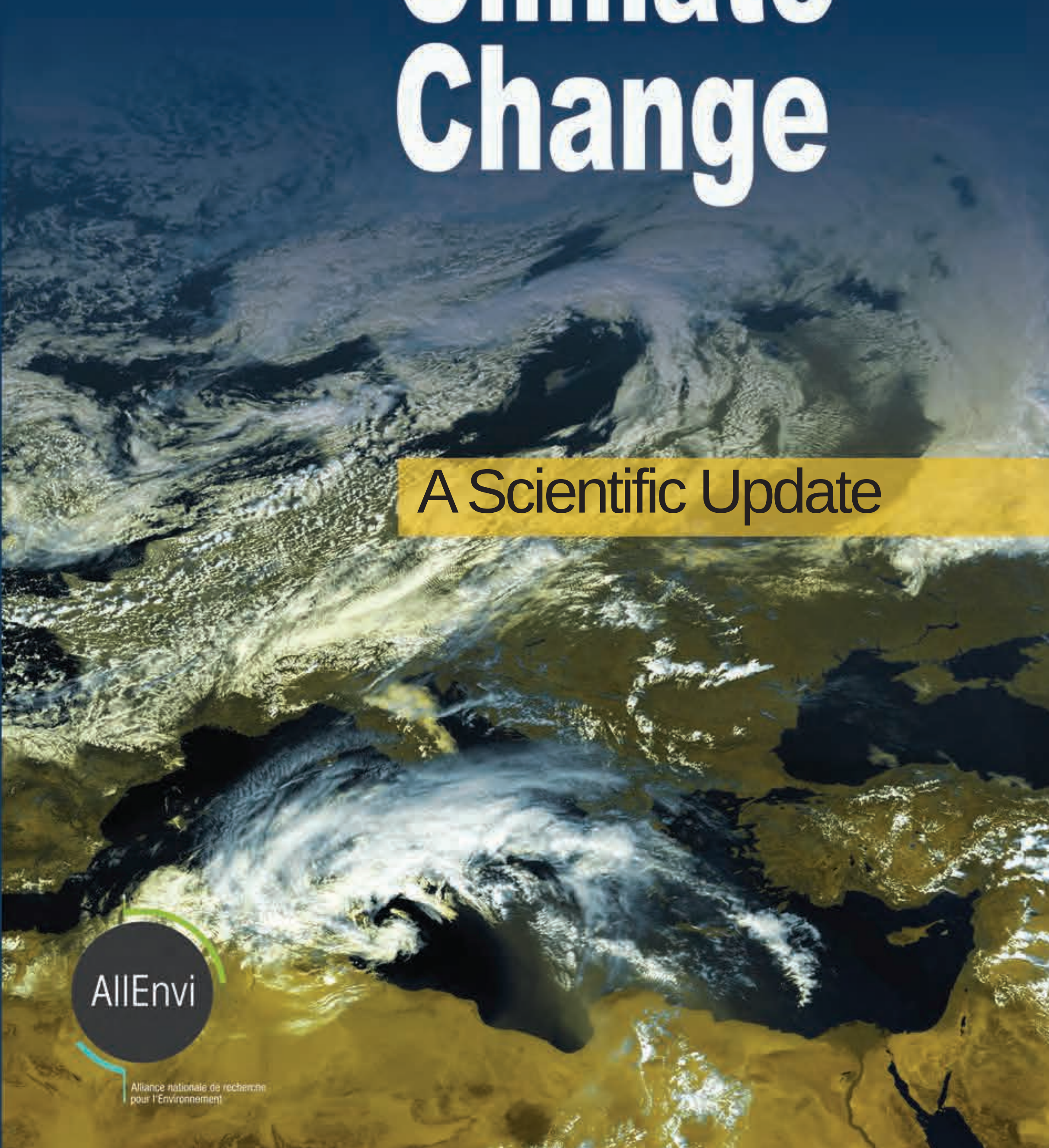
The Mediterranean Region under Climate Change

A Scientific Update



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A Scientific Update

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