Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study

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Climate change is significantly modifying ecosystem functioning on a global scale, but little is known about the response of deep-sea ecosystems to such change. In the past decade, extensive climate change has modified the physico-chemical characteristics of deep waters in the eastern Mediterranean. Climate change has caused an immediate accumulation of organic matter on the deep-sea floor, altered the carbon and nitrogen cycles and has had negative effects on deep-sea bacteria and benthic fauna. Evidence from a miniature ocean model provides new ways of interpreting signals from the deep sea and indicates that, contrary to what might have been expected, deep-sea ecosystems do respond quickly to climate change.

There is an increasing awareness that the environment of the Earth is changing, but it is unknown whether these changes occur cyclically, stochastically, episodically or are long-term trends. Although our knowledge of some short-lived events (e.g. the El Niño Southern Oscillation (ENSO) event) that have been proven to induce significant modifications in the structure and functioning of ecosystems is improving, the role of climatic variations in regulating marine populations and communities is not well understood.

There are indications that marine systems respond to climate change: temperature variations, for example, do not only affect metabolic rates of marine organisms, but also influence other important environmental variables, such as local currents, water column stratification, nutrient cycling and primary production. These variables strongly affect population and community dynamics and, over time, community structure and function.

Major studies of the effects of climate change on marine ecosystems have taken place in the Pacific Ocean and many of them have focused on the consequences of ENSO events. ENSO is the result of a cyclic warming and cooling of the surface ocean of the central and eastern Pacific. During El Niño years, the influence of upwelling cold waters decreases, causing the surface waters of the central and eastern Pacific to warm up. By contrast, when the upwelling of cold deep waters is more intense than usual, the so-called La Niña event takes place. ENSO events have been proven to modify the structure and productivity of the pelagic ecosystem at extremely large spatial scales. During El Niño events, the increased water column stratification inhibits nutrient upwelling, causes a decrease of primary production, zooplankton abundance and larval fish productivity and modifies the planktonic food-web structure. El Niño-related climatic events also affect coastal benthic community production and structure, and the opposite effects probably occur as a result of La Niña-related events.

Climatically driven ecosystem disturbance has also been recently reported in coastal areas of the western Mediterranean, where the anomalous increase of summer temperatures (of −2–3°C) and the deepening of the thermocline have resulted in a massive mortality of the benthic fauna (e.g. sponges and gorgonians) inhabiting hard substrates. Mortality was attributed not only to the surface water warming per se, but also to the stability of high sea temperatures over long periods (i.e. several months). A similar climate-induced disturbance was observed in the Indian Ocean and along the Caribbean coastline, where the increase of water temperature over an extended period resulted in extensive coral bleaching and mortality.

Compared with terrestrial ecosystems, in which the response to climate change is increasingly apparent, evidence of ecosystem response in the oceans is difficult to obtain. This applies particularly to the deep sea, where the need for expensive high-tech sampling devices limits the acquisition of long-term data. Therefore, only a few studies have examined the effects of current climate changes on the deep sea.

Recently, large changes in the physico-chemical characteristics of the eastern Mediterranean deep water, known as the 'Transient event', have been reported. Long-term investigations of deep-sea biology have been carried out in the eastern Mediterranean, providing a unique opportunity to study the response of a deep-sea ecosystem to climate variability on a decadal scale. Because the Mediterranean Sea behaves as a miniature ocean, changes that occur in the eastern Mediterranean can be used as a model of the potential instability of the oceanic circulation. Such a model would help our understanding and our predictions of the impact of climate change in deep seas worldwide.
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Fig. 1. Changes in factors affecting the quality of sedimentary organic matter from 1989–1998 measured in deep-sea sediments (at depths of 950 m (squares) and 1540 m (circles)) of the Cretan Sea(43,45,46). (a) Trends in chlorophyll a concentrations from January 1989 to September 1997; (b) trends in organic C (yellow) and protein (green) concentrations from January 1989 to September 1997; (c) trends in the carbon:nitrogen (C:N) (yellow) and protein:carbohydrate (green) ratios from January 1989 to September 1997; Bars indicate standard deviations.

Climate-induced physico-chemical changes in the deep sea
Deep-sea ecosystems (excluding hydrothermal vents) are thought to be extremely stable compared with coastal environments. With the exception of hydrostatic pressure and hydrodynamic forcing (current energy and benthic storms), the main feature of deep seas is a very narrow range of temperature and salinity, which, at any given depth, remains almost constant with time(44).

Climate forcing causes surface waters to become denser and to sink as a result. Thus, the characteristics of deep waters are originally determined by the prevailing surface climatic conditions, although these are modified by subsequent mixing. Consequently, any major change in surface climate can be expected to influence deep-water characteristics(45). Climate-induced changes in deep seas occur in two ways: (1) by deep-water warming, linked to surface temperature increases and to intermediate layer warming; and (2) by the formation of new deep waters, which occurs when surface waters, preconditioned by high salinity, become sufficiently dense by cooling to cause them to sink.

Both kinds of climate-induced change have been recorded in the Mediterranean. A general warming trend has been observed in the deep waters of the western Mediterranean, where water temperatures have increased by ~0.12°C in the past 30 years as a possible result of greenhouse gas-induced global warming(46). The opposite effect occurred in the past decade in the eastern Mediterranean as a response to regional variability in atmospheric forcing(47). Changes in the deep waters in this area occurred in two phases(21,27): the first, between 1987 and 1992, was characterized by a massive formation of dense, relatively warm water in the south Aegean (the Cretan Deep Water), mainly as a result of increased salinity; the second phase, from 1992 to 1994, was characterized by a drop in deep-water temperature of ~0.4°C, which resulted in even denser deep water being formed(21,27,28). Consequently, the old eastern Mediterranean Deep and Bottom Waters were uplifted by several hundred metres(21,27) and formed a distinct nutrient-rich intermediate-water layer (the Transitional Mediterranean Water)(27,29), which, under the influence of cyclonic circulation, reached shallower depths (100–150 m; i.e. close to the euphotic zone(28–30)).

Pelagic-benthic coupling and deep-sea biogeochemical changes
Life in the deep sea depends on the constant rain of settling particles produced in the photic zone and/or exported from the continental shelf(24). The eastern Mediterranean is considered to be one of the most oligotrophic areas of the world and is characterized by extremely low primary productivity (20–25 g carbon (C) m⁻² yr⁻¹) and, as a result, extremely small amounts of primary organic matter reach the sea floor(32).

However, the Transient event and the consequent uplift of nutrient-rich deep waters in the eastern Mediterranean resulted in increased biological production. From the early 1980s to the 1994–1995 season(31,33) (i.e. after cooling), primary productivity over the continental shelf and upper slope increased threefold, reaching values comparable with those in mesotrophic environments (i.e. 60–80 g C m⁻² yr⁻¹)(33). Such changes in primary productivity were also coupled with changes in phytoplankton assemblage composition (measured as the diatom:centric flagellate ratio), species dominance and average phytoplankton cell size (which increased by between two and five times)(33,34). Increased primary production and phytoplankton cell size are known to enhance vertical fluxes of phytodetritus and organic C to deep-sea sediments(35). This was observed in the eastern Mediterranean, where phytodetritus input to the deep-sea floor increased by up to two orders of magnitude(26) (Fig. 1a). This flux determined an accumulation of organic C and N on the sea floor(26) (Fig. 1b) and enhanced the quality of sedimentary organic matter, evident in terms of protein accumulation (Fig. 1b), increased the total protein:carbohydrate content ratio and decreased the C:nitrogen (N) ratio (Fig. 1c, Box 1). Such phenomena are opposite to those described during El Niño events, in which a reduced export production from the euphotic zone has been reported(27,10,37,38).
Box 1. Organic matter availability in deep-sea ecosystems

With the exception of hydrothermal vents and cold seeps, deep-sea benthic ecosystems depend for their sustenance on the rain of particulate organic matter produced in the photic layer. During their descent through the water column, sinking particles are subjected to a progressive degradation, which reduces the quantity and quality of the organic material reaching the deep-sea bed. Only ~1–3% of the organic carbon produced by photosynthesis in the photic layer is exported to the deep seas. These particles are mainly composed of dead or senescent phytoplankton, zooplankton, and other debris of marine and terrestrial origin. When organic matter reaches the sediment surface, it is subjected to complex biotic and abiotic transformations, which alter its chemical composition, calorific content, and nutritional value.

Organic matter is composed of labile (simple sugars, fatty acids, and proteins) and refractory (humic and fulvic acids and structural carbohydrates) compounds in variable proportions. Only labile molecules are directly utilized as a food source by benthic consumers, whereas refractory molecules require an ageing process and conversion into low molecular weight compounds. This process is largely mediated by bacteria. Organic matter quality and its potential availability (i.e., its food value for consumers) has historically been determined using the carbon:nitrogen (C:N) ratio. As organic N (protein) is more readily utilized than organic C, low values of C:N (<10–15) indicate a high potential food availability, whereas higher values suggest the dominance of refractory compounds. A similar (reversed) approach has been based on the protein:carbohydrate ratio in the sediment: the higher the protein:carbohydrate ratio, the higher the food availability for consumers.

Proteins are key molecules in the nutritional requirement of all benthic consumers. In deep-sea sediments, proteins are generally present in extremely low concentrations, thus representing a limiting factor to the distribution, metabolism, and growth of benthic organisms.

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Climatically driven deep-sea biological disturbance

Previous studies have shown that the input of organic material to the marine sediment rapidly enhances benthic metabolism and secondary production and determines an increased density of deep-sea benthic organisms. These effects should be even more evident in food-limited environments, such as highly oligotrophic deep seas. However, exactly the opposite has been observed in the eastern Mediterranean. From 1989 to 1997, benthic bacteria, which in the eastern Mediterranean, account for most of the total benthic biomass, decreased by as much as 90% (Fig. 2a). This decrease was coupled with a large reduction in the total number of dividing bacteria and consequently a reduced bacterial turnover (which decreased by ~50%) and the availability of labile organic compounds. However, recent studies have also demonstrated that deep-sea bacteria are stenotherms, and display a reduction in growth rate with decreasing temperature.

Reduced bacterial density and activity, together with the trend of decreasing oxygen levels in deep waters, have contributed to the reduced remineralization of organic matter and to its accumulation in marine sediments. Such significant accumulation of nonconsumed and/or nonmineralized organic loads indicates a modification of the steady-state conditions of the C and N cycles in the deep sea. After 1994, the physical characteristics of the deep waters investigated tended to stabilize at new values. This was reflected by patterns of organic C, the C:N ratio and bacterial density, which also stabilized during this period, providing more evidence for a tight coupling between physical and biological processes.

Climatically driven biological disturbance was also observed for meiofauna. Meiofauna comprise 22 of the 40 animal phyla and are composed of the small organisms

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The Mediterranean ecosystem of the eastern basin has been characterized by its high biodiversity and productivity. However, recent climate-induced changes, such as warming, have potentially affected the distribution and abundance of benthic metazoans. These effects are expected to be different from those of deep-sea ecosystems that are subjected to climate-induced warming. El Niño events in the eastern Pacific, with rising sea surface temperatures, cause a deepening of the mixed layer, decreased nutrient concentrations in the surface waters, and reduced primary production and export of organic material towards the sea bed. During these warming events, therefore, deep-sea benthic ecosystems are likely to be subjected to more oligotrophic conditions as a result of altered plankton food-web structure. In this regard, recent studies carried out in the North Pacific have shown that, since the late 1970s, the increased sea surface temperature (1.5–3°C) has altered the surface productivity, reducing the supply of organic matter to sediments. These studies conclude that climate change has had a greater effect on benthic oxygen levels than changes in ocean circulation patterns.

Another potential source of change in deep seas, which can bias the interpretation of the relationship between climate change and ecosystem response, is the

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Spatial heterogeneity is an important source of variability of benthic parameters. In deep-sea sediments, chemical elements and living organisms can display a patchy distribution. The distribution of chemical elements is largely driven by physical processes (e.g. bottom currents and benthic storms), whereas the distribution of the living biota is also controlled by biologically mediated disturbances (e.g. predation), which create environmental heterogeneity favouring the aggregation of organisms. These processes occur at different spatial scales. At a large scale, physical processes are the main factors that regulate the distribution of benthic parameters, whereas at the local scale, the complex biological interactions within the food web dominate.

Investigations carried out in the eastern Mediterranean have revealed an extremely low micro- (i.e. at the cm scale between sediment cores taken from the same area) and mesoscale (i.e. 1–100 m scale in cores taken from different areas) spatial variability of the sediment parameters. In addition, no statistically significant differences have been observed on a larger spatial scale (i.e. at the km scale, between sampling sites at similar depths). The temporal variability of chemical elements and living biota in deep seas are linked to the organic matter produced in the euphotic zone. The fraction of this production that escapes the euphotic zone as particulate organic matter sinking into the deep sea also exhibits temporal variability, reflecting the changes in surface water production. Long time series measurements of particulate fluxes and benthic variables (e.g. phytodetritus deposition, faunal density and biomass and community structure) in the deep sea have revealed the presence of seasonal and interannual changes. Interannual variability of biological processes generally becomes larger than seasonal variability when relevant interannual changes in environmental conditions occur as a result of episodic or stochastic events, or long-term climate change. Temporal analysis and comparisons between seasonal and interannual changes clearly indicate that the deep-sea ecosystem of the eastern Mediterranean exhibits limited variability among seasons that is almost negligible compared with changes observed on longer timescales (i.e. over a decade).

References


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When studying cause-effect relationships between variables, as in the case of the ecosystem response to climate change, high-quality data are essential. In particular, investigations of the benthic compartment (owing to the bidimensional characteristics of the substrate) require that seasonal and spatial variability are taken into account as another potential source of bias (Box 2).

Prospects

The effects of climate change on the oceans should be seen from both top-down and bottom-up perspectives. The increasing frequency of many deep-sea organisms recorded in shallow waters during the past three decades, possibly induced by climate change, confirms the existence of bidirectional interactions between the surface and deeper waters. However, because of the lack of information, it is not clear whether the deep sea responds rapidly to climate change or if there is a lag period. As Residence times of deep waters are of the order of several decades, recent studies have suggested that there should be a lag and that deep-sea organisms respond to climate changes that occurred several decades ago. However, the response from a miniature ocean model indicates that climatic change could have a more rapid effect on deep-sea ecosystem functioning.

From the information available, it is emerging that deep-sea ecosystems are fragile and that deep-sea communities are extremely sensitive to a wide range of disturbances. Even relatively small changes in the physical characteristics of deep waters might alter the steady state of important biogeochemical and functional variables. There is still little information about the long-term (i.e. decades to centuries) variability of several deep-sea parameters (e.g. temperature, salinity, bottom currents, organic and inorganic nutrients) and, without knowing about long-term trends, the effect of climate change on deep-sea ecosystem functioning cannot be predicted. Recent studies of deep-sea coral banks indicate that these colonies, which have lifespans of several centuries, can provide deep-sea records of climate change. This promising new information should satisfy the need for long-term data on changing climatic conditions, but the deep-sea ecosystem response to such changes is still largely unknown.

As deep seas cover over 50% of the surface of the Earth and drive biogeochemical cycles on a global scale, investigating climate-induced changes in the deep sea is crucial to our understanding and ability to predict the consequences of climate change.
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