

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

Roberto Danovaro, Antonio Dell'Anno, Mauro Fabiano, Antonio Pusceddu and Anastasios Tselepidis

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 trends¹. 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 understood².

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 production³. 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^{4–6}. 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^{7–11}. El Niño-related climatic events also affect coastal benthic community production and structure^{12,13}, and the opposite effects probably occur as a result of La Niña-related events^{14,15}.

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)¹⁶. A similar climate-induced disturbance was observed in the Indian Ocean and along the Caribbean coastline, where the increase in water temperature over an extended period resulted in extensive coral bleaching and mortality^{17,18}.

Compared with terrestrial ecosystems, in which the response to climate change is increasingly apparent¹⁹, 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 sea²⁰.

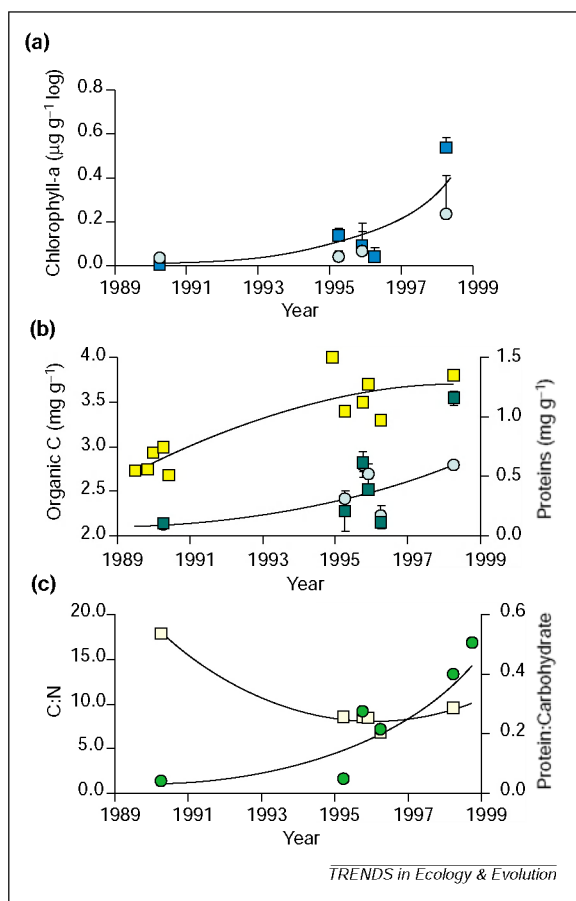
Recently, large changes in the physico-chemical characteristics of the eastern Mediterranean deep water, known as the 'Transient event', have been reported²¹. Long-term investigations of deep-sea biology have been carried out in the eastern Mediterranean, providing a unique opportunity to study the response of a deep-sea ecosystem to climate variability on a decadal scale. Because the Mediterranean Sea behaves as a miniature ocean²², 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 worldwide²³.

Roberto Danovaro*
Antonio Dell'Anno
Antonio Pusceddu
Institute of Marine
Science, University of
Ancona, Via Brece
Bianche, 60131 Ancona,
Italy.
*e-mail: danovaro@
popcsi.unian.it

Mauro Fabiano
DIPTERIS, University of
Genoa, Corso Europa 26,
16100 Genoa, Italy.

Anastasios Tselepidis
Institute of Marine
Biology of Crete, PO Box
2214, 71003 Heraklion,
Crete, Greece.

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 time²⁴.

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 characteristics²⁵. Climate-induced changes in deep seas can 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 warming²⁶. The opposite effect occurred in the past decade in the eastern Mediterranean as a response to regional variability in atmospheric forcing²³. 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 shelf²⁴. The eastern Mediterranean is considered to be one of the most oligotrophic areas of the world and is characterized by extremely low primary productivity [$20\text{--}25\text{ g carbon (C) m}^{-2}\text{ y}^{-1}$]³¹ and, as a result, extremely small amounts of primary organic matter reach the sea floor³². 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. $60\text{--}80\text{ g C m}^{-2}\text{ y}^{-1}$)³³. Such changes in primary productivity were also coupled with changes in phytoplankton assemblage composition (measured as the diatom:dinoflagellate 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 sediments³⁵. This was observed in the eastern Mediterranean, where phytodetritus input to the deep-sea floor increased by up to two orders of magnitude³⁶ (Fig. 1a). This flux determined an accumulation of organic C and N on the sea floor³⁶ (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^{7, 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^a. 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^b. These particles are mainly composed of dead or senescent phytoplankton, zooplankton moults 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 utilizable as a food source by benthic consumers, whereas refractory molecules require an ageing process and conversion into low molecular weight compounds^c. 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^d.

Proteins are key molecules in the nutritional requirement of all benthic consumers. In deep-sea sediments,

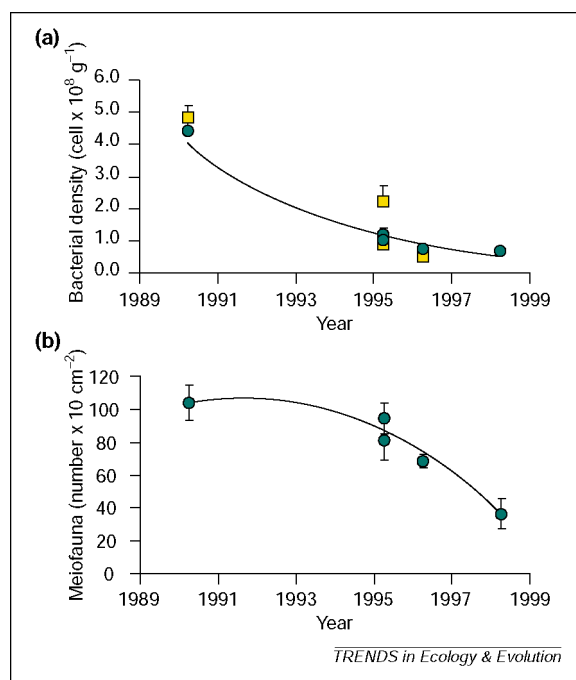
proteins are generally present in extremely low concentrations, thus representing a limiting factor to the distribution, metabolism and growth of benthic organisms^e.

References

- a Gage, J.D. and Tyler, P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-sea Floor*, Cambridge University Press
- b Lampitt, R.S. and Antia, A.N. (1997) Particle flux in deep seas: regional characteristics and temporal variability. *Deep Sea Res.* 144, 1377–1403
- c Henrichs, S.M. (1992) Early diagenesis of organic matter in marine sediments: progress and perplexity. *Mar. Chem.* 39, 119–149
- d Dell'Anno, A. *et al.* (2000) Enzymatically hydrolysed protein and carbohydrate pools in deep-sea sediments: estimates of the potentially bioavailable fraction and methodological considerations. *Mar. Ecol. Prog. Ser.* 196, 15–23
- e Danovaro, R. *et al.* (1999) Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions–Catalan Sea (western Mediterranean) and the Cretan Sea (eastern Mediterranean). *Progr. Oceanogr.* 44, 287–312

Fig. 2. Density of benthic bacteria and meiofauna from the sediments of the Cretan Sea [at 950 m (squares) and 1540 m (circles)]^{41,43,46,49,50}.

(a) Interannual changes in bacterial density in September 1989, 1994, 1995, 1997 and March 1998 (the exponential curve for 1540 m depth is shown); (b) interannual changes in meiofauna density at 1540 m depth in September 1989, 1994, 1995, 1997 and March 1998. Bars indicate standard deviations.



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 production³⁹ and determines an increased density of deep-sea benthic organisms⁴⁰. These effects should be even more evident in food-limited environments, such as highly oligotrophic deep seas³². 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 biomass⁴¹, 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%)³⁶. Bacteria are known to be heavily dependent upon both fluxes in organic C (Ref. 42) and the availability of labile organic compounds⁴³. However, recent studies have also demonstrated that deep-sea bacteria are stenotherms, and display a reduction in growth rate with decreasing temperature⁴⁴.

Reduced bacterial density and activity, together with the trend of decreasing oxygen levels in deep waters²⁹, 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 sea³⁶. After 1994, the physical characteristics of the deep waters investigated tended to stabilize at new values^{23,27,28}. This was reflected by patterns of organic C, the C:N ratio and bacterial density, which also stabilized during this period^{45,46}, providing more evidence for a tight coupling between physical and biological processes.

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

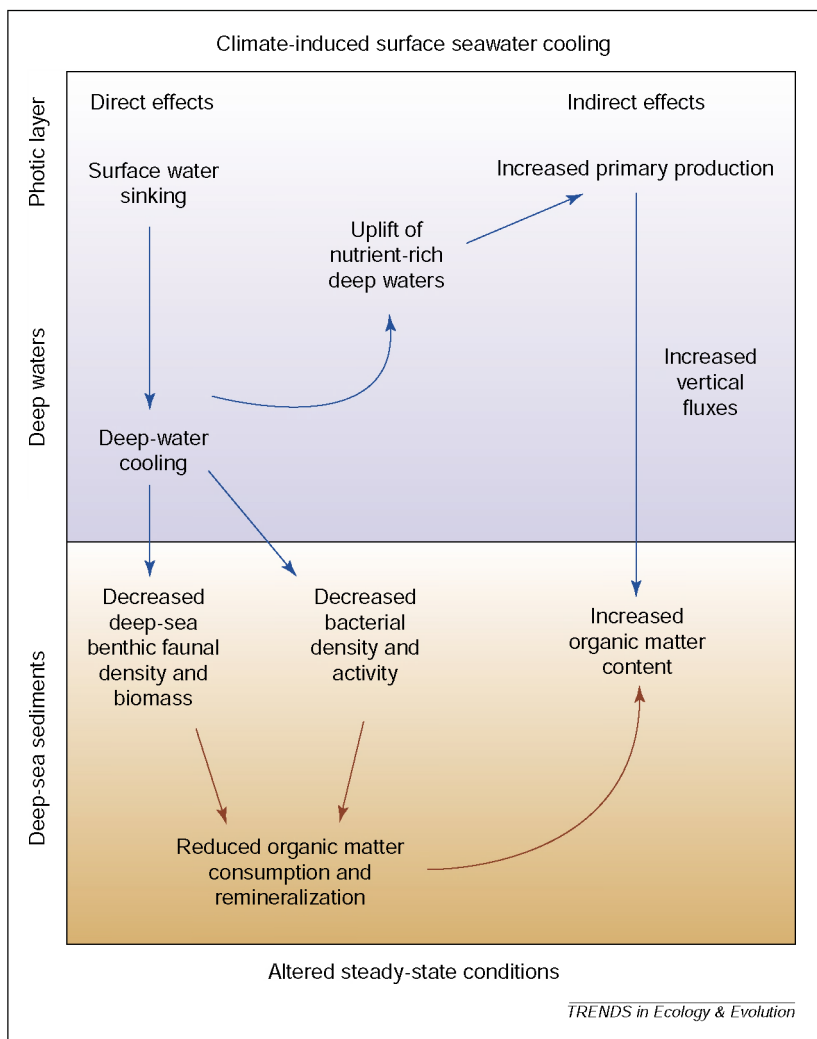


Fig. 3. Conceptual model of direct and indirect effects of climate-induced change on the deep-sea ecosystem of the eastern Mediterranean.

(30–500 μm) that represent the dominant component among benthic metazoans in all aquatic ecosystems⁴⁷. Nematodes account for 70–90% of the total density of deep-sea meiofauna. Because of their sensitivity to stressful conditions, lack of larval dispersal and high turnover rates, nematodes are considered to be useful bio-indicators in environmental monitoring⁴⁸ and could be used as a model for investigating metazoan responses to climate change.

After deep-water cooling, the deep-sea meiofauna in the eastern Mediterranean displayed a significant decrease in density (~65%, Fig. 2b). The decrease in meiofaunal biomass was even greater (by ~80%)^{49,50}. These data contrast with experimental and observational research demonstrating an increase in benthic organisms induced by phytodetrital accumulation on the sea bed^{39,40}. Despite the increased organic nutrient availability, changes in the physical characteristics of the water masses had a negative effect on the metazoan density and biomass.

The observed disturbance of meiofauna in the deep sea has two possible explanations. The first is a direct negative effect of water cooling on benthic metazoans. This explanation is supported by the long-term adaptation of deep-sea organisms to constant

temperature conditions⁵¹ – the abrupt decrease of even a few tenths of a degree centigrade might have affected their reproductive potential. The long duration of the deep-water cooling (over two years) enhanced the negative effects of the lower temperatures, especially on organisms with high turnover rates (nematodes have a short generation time, ranging from 4–63 days⁵²; during the cold period, there would potentially have been at least 12 and possibly over 200 generations).

The effect of temperature changes on deep-sea benthic fauna has been documented in the western Mediterranean, where macrofauna consist partly of reproductively sterile pseudopopulations that are maintained by a continuous larval inflow from mother populations inhabiting the colder deep Atlantic Ocean⁵³. The high temperature and high salinity of the Mediterranean bottom waters is thought to hamper the successful establishment of species arriving from the colder oceans. The same phenomenon has recently been observed in other areas of the Mediterranean (in the Ligurian and Tyrrhenian Seas), where the establishment of macrobenthic pseudopopulations and the mortality and/or introduction of certain species was attributed to temperature changes induced by climate forcing⁵⁴.

An alternative explanation for the observed climate change-induced impact on nematodes is the reduction of the microbial biomass and activity⁴⁸. Because nematodes, particularly in the deep sea, are either specific bacterial feeders or general microbial feeders, it is possible that the strong reduction of microbial biomass resulted in a reduction of suitable organic food sources.

From the overall deep-sea response to climate change in the eastern Mediterranean (Fig. 3), it is evident that the climate change taking place there has had direct (biological disturbance) and indirect (altered biogeochemical cycles) effects on the deep-sea ecosystem. 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^{7,9}. 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 patterns⁵⁵.

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

Box 2. Spatial heterogeneity and temporal variability in deep-sea sediments

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^a.

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^b. 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)^c.

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^d. 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)^e.

References

- a Schaff, T.R. and Levin, L.A. (1994) Spatial heterogeneity of benthos associated with biogenic structures on the North Carolina continental slope. *Deep Sea Res. II* 41, 901–918
- b Danovaro, R. *et al.* (1998) Heterotrophic nanoflagellates, bacteria and labile organic compounds in continental shelf and deep-sea sediments of the eastern Mediterranean. *Microb. Ecol.* 35, 244–255
- c Danovaro, R. *et al.* (1995) Meiofauna of the deep Eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. *Prog. Oceanogr.* 36, 329–341
- d Smith, K.L. and Druffel, E.R.M. (1998) Long time-series monitoring of an abyssal site in the NE Pacific: an introduction. *Deep Sea Res. II* 45, 573–586
- e Danovaro, R. *et al.* (1998) Long-term changes in deep-sea benthic ecosystems: the eastern Mediterranean case. In *Variability of the Mediterranean Sea* (Lykousis, V. and Sakellariou, D., eds), pp. 202–203, NCMR Press

presence of anthropogenic disturbance, either from construction activities on the shore, from resource exploitation or from other sources⁵⁶. None of these causes were evident in the deep eastern Mediterranean during the decade of observation. However, the growing direct human impact on oceanic systems has to be taken into account in future studies as a potentially important source of change in deep-sea ecosystem function⁵⁷.

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 change²⁵, 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 ago²⁵. 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 disturbances²⁴. 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 change⁵⁸. 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.

Acknowledgements

We thank A. Theocharis for providing information on climate-induced physical changes, F. Azam, G. Bavestrello, F. Boero, O. Carnevali, C. Cerrano, N. Della Croce, A. Eleftheriou, L. Ferrante, S. Fraschetti, C. Gambi, P. Giordani, E. Ignatiades, D. Marrale, E. Olmo, W. Roether, A. Russo, M. Serresi and two anonymous reviewers for discussion and constructive comments on this article. This study was supported by European Union CINCS (pelagic–benthic coupling in the oligotrophic Cretan Sea) and MATER (mass transfer and ecosystem response) programmes.

References

- 1 Eckmann, J.E. (1994) Modelling physical-biological coupling in the ocean: the U.S. GLOBEC Program. *Deep Sea Res.* **II** 41, 1–5
- 2 Fields, P.A. *et al.* (1993) Effects of expected global climate change on marine faunas. *Trends Ecol. Evol.* **8**, 361–367
- 3 McGowan, J.A. *et al.* (1998) Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* **281**, 210–217
- 4 Dayton, P.K. *et al.* (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* **8**, 309–322
- 5 Whitney, F.A. and Freeland, H.J. (1999) Variability in upper-ocean waters in the NE Pacific Ocean. *Deep Sea Res.* **II** 46, 2351–2370
- 6 Ishizaka, J. *et al.* (1997) Size and taxonomic plankton community structure and carbon flow at the equator, 175°E during 1990–1994. *Deep Sea Res.* **II** 44, 1927–1949
- 7 Thunell, R.C. (1998) Seasonal and annual variability in particle fluxes in the Gulf of California: a response to climate forcing. *Deep Sea Res.* **II** 45, 2059–2083
- 8 Barber, R.T. *et al.* (1996) Primary productivity and its regulation in the equatorial Pacific during and following the 1991–1992 El Niño. *Deep Sea Res.* **II** 43, 933–969
- 9 Barber, R.T. and Chavez, F.P. (1986) Ocean variability in relation to living resources during the 1982–83 El Niño. *Nature* **319**, 279–285
- 10 Baldwin, R.J. *et al.* (1998) Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. *Deep Sea Res.* **II** 45, 643–665
- 11 Karl, D.M. *et al.* (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. *Nature* **373**, 230–234
- 12 Dayton, P.K. *et al.* (1999) Temporal and spatial scales of kelp demography: the role of oceanic climate. *Ecol. Monogr.* **69**, 219–250
- 13 Connolly, S.R. and Roughgarden, J. (1999) Increased recruitment of northeast Pacific barnacles during the 1997 El Niño. *Limnol. Oceanogr.* **44**, 466–469
- 14 Hayward, T.L. *et al.* (1999) The state of the California current in 1998–1999: transition to cool-water conditions. *Reports of California Cooperative Oceanic Fisheries Investigations* **40**, 29–62
- 15 Mackey, D.J. *et al.* (1997) Phytoplankton productivity and the carbon cycle in the western Equatorial Pacific under El Niño and non-El Niño conditions. *Deep Sea Res.* **II** 44, 9–10
- 16 Romano, J.C. *et al.* (2000) Anomalie thermique dans les eaux du golfe de Marseille durant l'été 1999. Une explication partielle de la mortalité d'invertébrés fixés? *C.R. Acad. Sci.* **323**, 415–427
- 17 Pockley, P. (2000) Global warming identified as main threat to coral reefs. *Nature* **407**, 932
- 18 Aronson, R.B. *et al.* (2000) Coral bleach-out in Belize. *Nature* **405**, 36
- 19 Pounds, J.A. *et al.* (1999) Biological response to climate change on a tropical mountain. *Nature* **398**, 611–615
- 20 Lehodey, P. and Grandperrin, R. (1996) Influence of temperature and ENSO events on the growth of the deep demersal fish *Alfonsino*, *Beryx splendens*, off New Caledonia in the western tropical South Pacific Ocean. *Deep Sea Res.* **II** 43, 49–57
- 21 Roether, W. *et al.* (1996) Recent changes in Eastern Mediterranean deep waters. *Science* **271**, 333–335
- 22 Bethoux, J.P. *et al.* (1999) The Mediterranean Sea: a miniature ocean for climatic and environmental studies and a key for the climatic functioning of the North Atlantic. *Prog. Oceanogr.* **44**, 131–146
- 23 Lascaratos, A. *et al.* (1999) Recent changes in deep water formation and spreading in the eastern Mediterranean Sea: a review. *Prog. Oceanogr.* **44**, 5–36
- 24 Gage, J.D. and Tyler, P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-Sea Floor*, Cambridge University Press
- 25 Van der Spoel, S. (1994) A warning from the deep. *Prog. Oceanogr.* **34**, 207–210
- 26 Bethoux, J.P. *et al.* (1990) Warming trend in the Western Mediterranean deep water. *Nature* **347**, 660–662
- 27 Theoharis, A. *et al.* (1999) Climatic changes in the Aegean Sea influence the eastern Mediterranean thermohaline circulation (1986–1997). *Geophys. Res. Lett.* **26**, 1617–1620
- 28 Theoharis, A. *et al.* (1999) A synthesis of the circulation and hydrography of the South Aegean Sea and the Straits of the Cretan Arc (March 1994–January 1995). *Prog. Oceanogr.* **44**, 469–509
- 29 Souvermezoglou, E. *et al.* (1999) Temporal variability in oxygen and nutrient concentrations in the southern Aegean Sea and the Straits of the Cretan Arc. *Prog. Oceanogr.* **44**, 573–600
- 30 Klein, B. *et al.* (1999) The large deep water transient in the Eastern Mediterranean. *Deep Sea Res.* **46**, 371–414
- 31 Dugdale, R.C. and Wilkerson, F.R. (1988) Nutrient sources and primary production in the Eastern Mediterranean. *Oceanol. Acta* **9**, 178–184
- 32 Danovaro, R. *et al.* (1999) Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions–Catalan Sea (western Mediterranean) and the Cretan Sea (eastern Mediterranean). *Prog. Oceanogr.* **44**, 287–312
- 33 Psarra, S. *et al.* (2000) Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Prog. Oceanogr.* **46**, 187–204
- 34 Siokou-Fragou, I. *et al.* (1999) Plankton characteristics in the Aegean, Ionian and NW Levantine Seas. In *The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems* (Malanotte-Rizzoli, P. and Eremeev, V.N., eds), pp. 205–223, NATO Science Series 2 Environmental Security 51
- 35 Boyd, P. and Newton, P. (1995) Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. *Deep Sea Res.* **42**, 619–639
- 36 Danovaro, R. *et al.* (1998) Long-term changes in deep-sea benthic ecosystems: the eastern Mediterranean case. In *Variability of the Mediterranean Sea* (Lykousis, V. and Sakellariou, D., eds), pp. 202–203, NCMR Press
- 37 Barber, R.T. and Chavez, F.P. (1983) Biological consequences of El Niño. *Science* **222**, 1203–1210
- 38 Wong, C.S. *et al.* (1999) Seasonal and interannual variability in particle fluxes of carbon, nitrogen and silicon from time series of sediment traps at Ocean Station P, 1982–1993: relationship to changes in subarctic primary productivity. *Deep Sea Res.* **II** 46, 2735–2760
- 39 Graf, G. (1989) Benthic–pelagic coupling in a deep-sea benthic community. *Nature* **341**, 437–439
- 40 Gooday, A.J. (1988) A benthic foraminiferal response to the deposition of phytodetritus in the deep sea. *Nature* **332**, 70–73
- 41 Danovaro, R. *et al.* (2000) Bacterial response to seasonal changes in labile organic matter composition on the continental shelf and bathyal sediments of the Cretan Sea. *Prog. Oceanogr.* **46**, 345–366
- 42 Deming, J.W. and Yager, P.L. (1992) Natural bacterial assemblages in deep-sea sediments: towards a global view. In *Deep-sea Food Chains and Global Carbon Cycle* (Rowe, G.T. and Pariente, V., eds), pp. 11–27, Kluwer Academic Publishers
- 43 Danovaro, R. *et al.* (1993) Labile organic matter and microbial biomasses in deep-sea sediments (Eastern Mediterranean Sea). *Deep Sea Res.* **40**, 953–965
- 44 Yayanos, A.A. (1995) Microbiology to 10 500 meters in the deep sea. *Annu. Rev. Microbiol.* **49**, 777–805
- 45 Tselepidis, A. *et al.* (2000) Organic matter composition of the continental shelf and bathyal sediments of the Cretan Sea (NE Mediterranean). *Prog. Oceanogr.* **46**, 311–344
- 46 Danovaro, R. *et al.* (1999) Biochemical composition of sedimentary organic matter and bacterial distribution in the Aegean Sea: trophic state and pelagic–benthic coupling. *J. Sea Res.* **42**, 117–129
- 47 Higgins, R.P. and Thiel, H. (1988) *Introduction to the Study of Meiofauna*, Smithsonian Institution Press
- 48 Bongers, T. and Ferris, H. (1999) Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol. Evol.* **14**, 224–228
- 49 Danovaro, R. *et al.* (1995) Meiofauna on the deep eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. *Prog. Oceanogr.* **36**, 329–341
- 50 Danovaro, R. *et al.* (2000) Dynamics of meiofaunal assemblages on the continental shelf and deep-sea sediments of the Cretan Sea (NE Mediterranean): relationships with seasonal changes in food supply. *Prog. Oceanogr.* **46**, 367–400
- 51 Somero, G.N. (1992) Biochemical ecology of deep-sea animals. *Experientia* **48**, 537–543
- 52 Vranken, G. *et al.* (1986) *A Re-evaluation of Marine Nematode Productivity*, International Council for the Exploration of the Sea, Copenhagen, Denmark
- 53 Bouchet, P. and Taviani, M. (1992) The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? *Deep Sea Res.* **39**, 169–184
- 54 Astraldi, M.F. *et al.* (1995) Climatic fluctuations, current variability and marine species distribution: a case study in the Ligurian Sea (north-west Mediterranean) *Oceanol. Acta* **18**, 139–149
- 55 Stott, L.D. *et al.* (2000) Increased dissolved oxygen in Pacific intermediate waters due to lower rates of carbon oxidation in sediments. *Nature* **407**, 367–370
- 56 Van-Dover, C.L. *et al.* (1992) Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. *Nature* **360**, 153–156
- 57 Morri, C. and Bianchi, C.N. (2001) Recent changes in biodiversity in the Ligurian Sea (NW Mediterranean): is there a climatic forcing? In *Mediterranean Ecosystems: Structures and Processes* (Faranda, F.M. *et al.*, eds), pp. 375–384, Springer-Verlag
- 58 Smith, J.E. *et al.* (1997) Rapid climate change in the North Atlantic during the Younger Dryas recorded by deep-sea corals. *Nature* **386**, 818–820