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

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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[1]. 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[2].

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[3]. 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 apparent[19], 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[20].

Recently, large changes in the physico–chemical characteristics of the eastern Mediterranean deep water, known as the 'Transient event', have been reported[21]. 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[22], 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[23].

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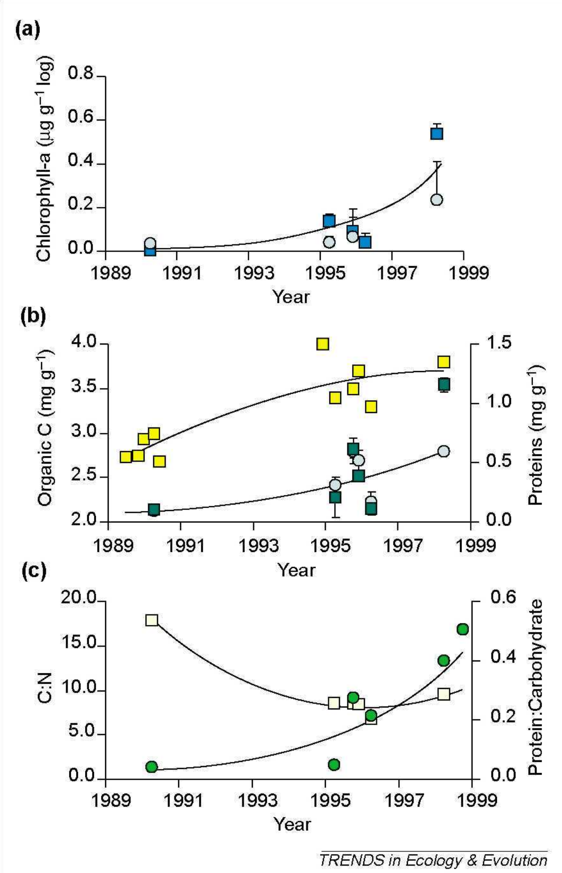

Fig. 1. Changes in factors affecting the quality of sedimentary organic matter from 1989–1998 measured in deep-sea sediments [at depths of 950 m (squares) and 1540 m (circles)] of the Cretan Sea[43,45,46]. (a) Trends in chlorophyll *a* concentrations from January 1989 to September 1997; (b) trends in 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[24].

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[25]. 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 warming[26]. The opposite effect occurred in the past decade in the eastern Mediterranean as a response to regional variability in atmospheric forcing[23]. 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} y^{-1}][31] 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} 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 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[36] (Fig. 1a). This flux determined an accumulation of organic C and N on the sea floor[36] (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. I* 44, 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 Mediterrranean). *Progr. Oceanogr.* 44, 287–312

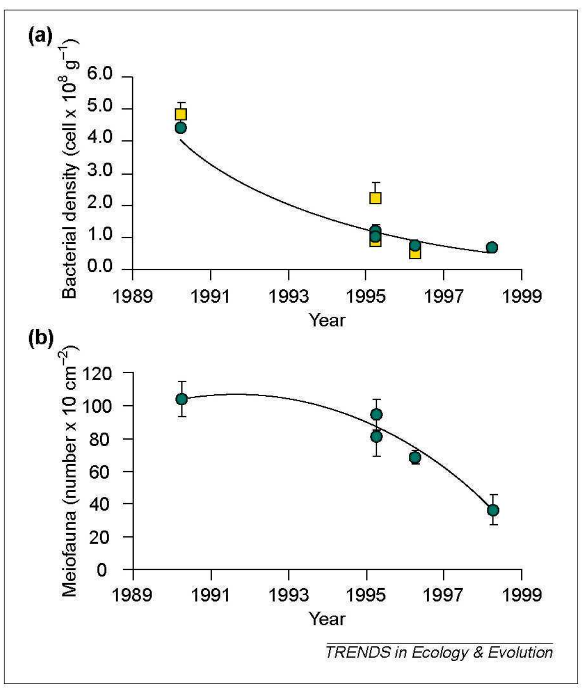

Fig. 2. Density of benthic bacteria and meiofauna from the sediments of the Cretan Sea [at 950 m (squares) and 1540 m (circles)][41,43,46,49,50]. (a) Interannual changes in bacterial density in September 1989, 1994, 1995, 1997 and March 1998 (the exponential curve for 1540 m depth is shown); (b) interannual 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 production[39] and determines an increased density of deep-sea benthic organisms[40]. These effects should be even more evident in food-limited environments, such as highly oligotrophic deep seas[32]. 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[41], 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 compounds[43]. However, recent studies have also demonstrated that deep-sea bacteria are stenotherms, and display a reduction in growth rate with decreasing temperature[44].

Reduced bacterial density and activity, together with the trend of decreasing oxygen levels in deep waters[29], 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[36]. 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

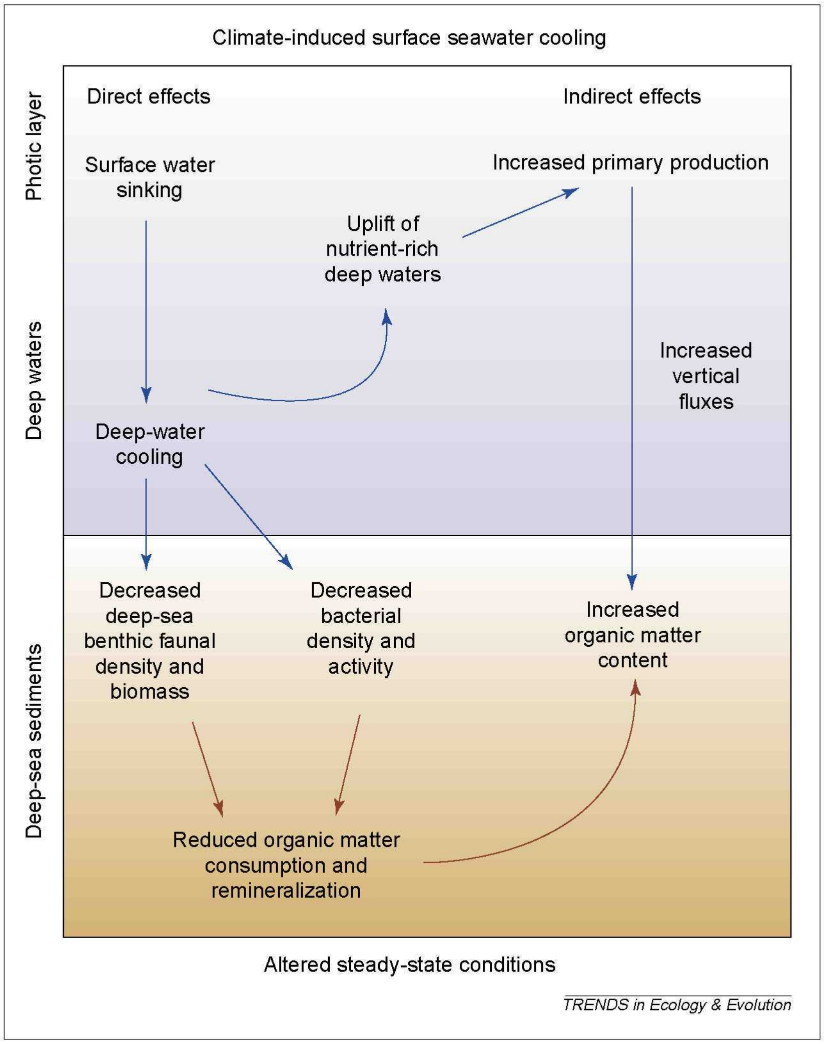

Fig. 3. Conceptual model of direct and indirect effects of climate-induced change on the deep-sea ecosystem of the eastern Mediterranean.

(30–500 μm) that represent the dominant component among benthic metazoans in all aquatic ecosystems[47]. 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 monitoring[48] 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 conditions[51] – 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 days[52]: 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 Ocean[53]. 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 forcing[54].

An alternative explanation for the observed climate change-induced impact on nematodes is the reduction of the microbial biomass and activity[48]. 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 patterns[55].

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. *Progr. 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* (Lykoussis, 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 sources[56]. 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 function[57].

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[25], 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[25]. 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[24]. 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[58]. 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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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 termique 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. *Progr. 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. *Progr. 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. *Progr. Oceanogr.* 34, 207–210
26 Bethoux, J.P. *et al.* (1990) Warming trend in the Western Mediterranean deep water. *Nature* 347, 660–662
27 Theocharis, 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 Theocharis, 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). *Progr. 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. *Progr. Oceanogr.* 44, 573–600
30 Klein, B. *et al.* (1999) The large deep water transient in the Eastern Mediterranean. *Deep Sea Res. I* 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 Mediterrranean). *Progr. Oceanogr.* 44, 287–312
33 Psarra, S. *et al.* (2000) Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Progr. 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. I* 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* (Lykoussis, 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. *Progr. 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. I* 40, 953–965
44 Yayanos, A.A. (1995) Microbiology to 10 500 meters in the deep sea. *Annu. Rev. Microbiol.* 49, 777–805
45 Tselepides, A. *et al.* (2000) Organic matter composition of the continental shelf and bathyal sediments of the Cretan Sea (NE Mediterranean). *Progr. 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. *Progr. 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. *Progr. 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. I* 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 oxydation 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

might play in the deep-sea ecosystem processes of the eastern Mediterranean Sea [1]. Hence, consideration must also be given to the climatic variability associated with the NAO and AO.

With regards to the ecology of the eastern Mediterranean Sea, the community structure of free-living bacteria in the Aegean Sea [10] (referred to as operational taxonomic units), suggests the presence of a distinct deep-water, compositionally complex, free-living (and to a lesser extent attached) bacterial community in the absence of temperature as a potential regulating factor. Recently, bacteria–phytoplankton coupling in the eastern Mediterranean Sea has been related to changes therein of the trends of bacterial and phytoplankton production [11]. How can these changes be related to biogeochemical cycles and climatic variability? A longer time series of data is needed if we expect to draw robust statistical inferences linking the ongoing decadal variability that characterizes climatic oscillations, such as the NAO and the AO, to the ecosystem dynamics in the eastern Mediterranean deep-sea, the Mediterranean basin and the adjacent North Atlantic.

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References

1 Danovaro, R. *et al.* (2001) Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. *Trends Ecol. Evol.* 16, 505–510
2 Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitations. *Science* 269, 676–679
3 Thompson, D.W.J. and Wallace, J.M. (1998) The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophys. Res. Lett.* 25, 1297–1300
4 Ward, M.N. (1996) Local and remote climate variability associated with East Mediterranean surface temperature anomalies. In *Proceedings of Conference on Mediterranean Forecasting* (eds), pp. 16–25, European. Science Foundation
5 Tsimplis, M.N. and Josey, S.A. (2001) Forcing of the Mediterranean Sea by atmospheric oscillations over the North Atlantic. *Geophys. Res. Lett.* 28, 803–806
6 Raicich, F. (2000) Variability in the Mediterranean Sea: connection with climatic patterns. The Eastern Mediterranean Climatic Transient, *CIESM Workshop Ser.* 10, 35–36
7 Vignudelli, S. *et al.* (1999) A possible influence of the North Atlantic Oscillation on the circulation of the Western Mediterranean Sea. *Geophys. Res. Lett.* 26, 623–626
8 Wu, P. *et al.* (2000) Towards an understanding of deep-water renewal in the Eastern Mediterranean. *J. Phys. Oceanogr.* 30, 443–458
9 Krom, M.D. *et al.* (1992) Nutrient dynamics and new production in a warm-core eddy from the Eastern Mediterranean-Sea. *Deep Sea Res. A.* 39, 467–480
10 Moeseneder, M.M. *et al.* (2001) Horizontal and vertical complexity of attached and free-living bacteria of the eastern Mediterranean Sea, determined by 16S rDNA and 16S rRNA fingerprints. *Limnol. Oceanogr.* 46, 95–107
11 Turley, C.M. *et al.* (2000) Relationship between primary producers and bacteria in an oligotrophic sea-the Mediterranean and biogeochemical implications. *Mar. Ecol. Progr. Ser.* 193, 11–18

Where is the climate?

Response from Danovaro, Dell'Anno, Pusceddu, Fabiano and Tselepides

We provided an ecological perspective of the possible influence of climate change on the deep sea, the largest ecosystem on Earth [1]. Although trying to understand how climate forcing originated is important, this was not the scope of our review. Conversely, Belgrano [2] focuses attention on the possible climatic forcing that might be related to changes in the physicochemical characteristics of the eastern Mediterranean. We documented how deep-sea ecosystems respond to actual temperature and salinity changes observed on a decadal scale, but we did not wish to infer on possible cause–effect relationships between the wintertime variability in the Mediterranean Sea and major climatic oscillations. Although the North Atlantic Oscillation (NAO) and the Arctic Oscillations (AO) might have a role in Eastern Mediterranean Transient (EMT) dynamics, this does not affect our ability to understand how the deep Eastern Mediterranean ecosystem responds to such changes. Very few examples are available for the deep sea and these are restricted to El Niño Southern Oscillation (ENSO) events. Ecologists always need longer time series to strengthen their conclusions, and this applies particularly to the deep sea where collecting long-term data is difficult and expensive. However, the EMT works as a model because physicochemical changes tend to recover to conditions before change within a decade. This model allows us to focus on the link between deep-sea ecosystem functioning and climate change rather than on long-term trends.

Belgrano also queries whether temperature is a relevant regulatory factor of bacterioplankton assemblages, using Moeseneder *et al.*'s work [3] as evidence. However, the conclusions Moeseneder *et al.*'s work [3] have nothing to do with the conclusions drawn by Belgrano, because the role of changing temperature in regulating the structure and activity of microbial assemblages was not tested by the former. Recent comparisons of bacterial and phytoplankton production in the western and eastern Mediterranean [4] do not allow us to draw conclusions about temporal trends related to climate change. Limited information is available on long-term effects of small temperature changes on the microbial components of food webs [5]. However, that a distinct assemblage of deep-sea benthic bacteria, adapted to steady-state conditions, is impacted by abrupt physicochemical changes is expected. We know much less about the extent and direction (positive or negative?) of such an impact and further work is needed from this perspective.

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References

1 Danovaro, R. *et al.* (2001) Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. *Trends Ecol. Evol.* 16, 505–510
2 Belgrano, A. (2002) Where is the climate? *Trends Ecol. Evol.* 17, XXX–XXX
3 Moeseneder, M.M. *et al.* (2001) Horizontal and vertical complexity of attached and free-living bacteria of the eastern Mediterranean Sea, determined by 16S rDNA and 16S rRNA fingerprints. *Limnol. Oceanogr.* 46, 95–107
4 Turley, C.M. *et al.* (2000) Relationship between primary producers and bacteria in an oligotrophic sea – the Mediterranean and biogeochemical implications. *Mar. Ecol. Progr. Ser.* 193, 11–18
5 Petchey, O.L. *et al.* (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402, 69–72

