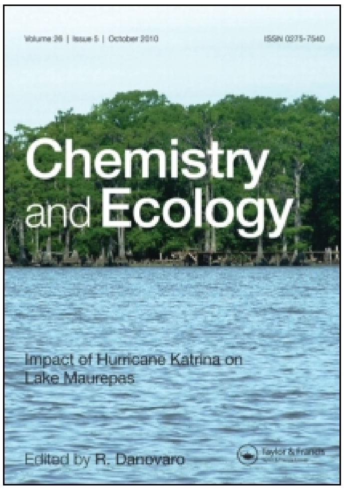
This article was downloaded by:
On: *15 January 2011*
Access details: *Access Details: Free Access*
Publisher *Taylor & Francis*
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Chemistry and Ecology

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

Organic inputs and ecosystem efficiency in the deep Mediterranean sea

Roberto Danovaro

Online publication date: 12 May 2010

To cite this Article Danovaro, Roberto(2003) 'Organic inputs and ecosystem efficiency in the deep Mediterranean sea', Chemistry and Ecology, 19: 5, 391 — 398
To link to this Article: DOI: 10.1080/02757540310001596681
URL: http://dx.doi.org/10.1080/02757540310001596681

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Chemistry and Ecology, Vol. 19(5), October 2003, pp. 391–398

Overview

ORGANIC INPUTS AND ECOSYSTEM EFFICIENCY IN THE DEEP MEDITERRANEAN SEA

ROBERTO DANOVARO*

Department of Marine Sciences, Polytechnic University of Marche,
Via Brecce Bianche, 60131, Italy

(Received 7 January 2003; In final form 11 June 2003)

Most studies on the benthic–pelagic coupling have focussed on how energy flow and fluxes of organic matter might influence the production and structure of the benthic communities. The classical scenario depicts the input of organic material from the photic zone fertilising the seabed and the consequent benthic nutrient regeneration supplying again the water column to sustain primary production processes. More recent studies highlighted the role of merobenthos as cysts of planktonic organisms that spend part of their life quiescent in the sediments. Such benthic propagules, when environmental conditions are not anymore adverse, can supply back plankton communities. Marine canyons might accumulate cysts derived from shelf export and reverse the direction of the coupling in a bottom up perspective. In the Mediterranean Sea, Eastern and Western basins display different productivity, flux rates and benthic standing stocks, with mass fluxes and organic carbon inputs up to 80 times higher in the Western basin. The low inputs reaching the deep-sea sediments are apparently responsible for the lack of coupling in the oligotrophic regions of the Eastern Mediterranean. The poverty of the organic input below 500 m, thought insufficient to fully support growth at the metazoan level, is partially balanced by a higher organic matter quality (*i.e.* bioavailability) in the more oligotrophic environments. In the Eastern Mediterranean, benthic organisms (*e.g.*, bacteria and small metazoans) are 2–3 times more efficient than in the Western Mediterranean in exploiting the available food sources. These conditions are reflected also by bioenergetic strategies. In the more oligotrophic eastern basin, meiofauna body composition (as lipid, protein and carbohydrate content) displays an apparent biochemical coupling with the composition of the organic food sources and is apparently able to cope with longer periods of scarce and highly unpredictable food inputs. Finally also climate changes might influence the pelagic-benthic coupling modifying primary productivity and sedimentation rates. Recent changes in deep water mass characteristics of the south Aegean, have determined the formation, apparently related to climate anomalies, of new colder and higher salinity water masses. These waters replaced and lifted up the older nutrient-reach deep waters, thus enhancing primary production and phytodetritus input to the deep sea. Such phenomenon has determined a clear accumulation (up to 10-times) of labile organic carbon in the deep sea. There is increasing evidence that greenhouse effects and transient climate changes might have rapid and profound effects also on pelagic–benthic coupling in deep-sea ecosystems.

Keywords: Organic matter inputs; Mediterranean Sea; Biodiversity; Ecosystem efficiency; Benthos; Trophodynamics

1 THE CONCEPT OF BENTHIC COUPLING TO ORGANIC INPUTS: TOP DOWN ORIENTED?

Deep-sea sediments are generally food-limited environments in which the abundance and distribution of benthic organisms is directly related to the amount of organic carbon reaching the

---

* Tel.: ++39 71 2204654; Fax: ++39 71 2204650; E-mail: danovaro@univpm.it

ISSN 0275-7540 print; ISSN 1029-0370 online
DOI: 10.1080/02757540310001596681

sediment surface (Gooday and Turley, 1990; Rowe, 1983; Thiel, 1983). In the recent years evidence has accumulated that all benthic components (from bacteria to megafauna) react to the POC flux from the photic layer (Graf, 1989; Deming and Yager, 1992; Danovaro *et al.*, 1998a). In studies relating primary productivity and carbon flux to benthic response it has also been hypothesised that the quality of the organic compounds in the rain of sinking POC was critical to metabolic processes (Rowe *et al.*, 1990). The amount of labile compounds (as readily digestible and/or utilisable organic matter) and in particular by protein availability in the deep sea may be a limiting factor the metabolism of most benthic organisms (Thiel, 1983; Pfannkuche and Thiel, 1987; Tietjen, 1992; Danovaro *et al.*, 1995). Sedimentation pulses of primary organic matter to the deep sea may vary in intensity between years and are often unpredictable (see Rice *et al.*, 1994; Wassmann *et al.*, 1996). Intensity, variability and quality of the nutrient inputs to the sea floor might have profound implications in the response of the different components of the benthic assemblages. Nonetheless, pelagic–benthic coupling studies in the deep sea are unclear as most of these studies fail to identify a significant benthic response to POM fluxes. Some authors hypothesise that benthic components might react to seasonal pulses of organic matter with some time delay (Pfannkuche, 1992; 1993; Pfannkuche and Lochte, 1993; Pfannkuche *et al.*, 1990). Gooday *et al.* (1996) have reported an apparent lack of response from benthic metazoans to phytodetritus deposition. One possible explanation for this phenomenon is the competition of bacteria and protozoa for the available resources. Studies on pelagic–benthic coupling have indeed shown that bacteria and protozoa, due to their shorter generation time might react to the sedimentation events with a rapid increase in abundance and biomass. The reason for the increasing importance of bacteria with increasing water depth could be searched in their ability of utilising a variety of inorganic nutrients and organic substrates, including refractory organic compounds, that might be not utilised by metazoans. Because bacteria are at the same time grazed by heterotrophic nanoflagellates and meiofauna, they contribute significantly to the direct transfer of recalcitrant detrital carbon to the higher trophic levels of the benthic food web (Danovaro *et al.*, 1998; Kemp, 1994). As bacteria have the highest carbon conversion efficiencies, this energy pathway would be a mechanism to optimise the exploitation of the available nutrient sources.

2 THE BOTTOM UP PERSPECTIVE

The classical concept of the pelagic–benthic as organic matter flux influencing the production and structure of the benthic communities includes also a bottom up perspective: the benthic nutrient regeneration and resuspension processes supply the water column to sustain again primary production processes. This simplified description doesn't take into account the relevance of the living specimens that might be resuspended from the sediments. Several studies have, indeed, made clear that individuals of many taxa previously thought to spend their entire life cycle in the water column actually rest in the seabed as cysts or resting stages for periods ranging from a single adverse season to decades or longer (Marcus *et al.*, 1994; Hairston *et al.*, 1996). These benthic resting stages enable the persistence of species, apparently disappeared, in the system and appear to be important agents of local re-colonization. Therefore, example of pelagic–benthic coupling is valid not only top down oriented but also bottom up directed as plankton communities might be supplied with organisms that were formerly benthic propagules. Marine canyons at the edges of continental shelves are sites where fine sediments and cysts accumulate from shelf export. If material from canyons can be reintroduced onto continental shelves via upwelling, then canyons might provide a source of recruits for coastal plankton communities. This integrated vision of pelagic–benthic coupling, defined by Marcus and Boero (1998) "supply vertical ecology", might open new perspectives also in terms of biodiversity. In fact all marine sediments contain extremely high densities of resting stages (densities of copepod resting eggs are typically in the order of $10^6\,m^{-2}$) and most of the are non-identified. Species considered extinct because they have not been recorded for several years may persist out of sign as resting stages (Boero *et al.*, 1996; Marcus and Boero, 1998). Organisms derived from propagules might include algae, such as dynoflagellates, that are responsible for noxious blooms. Red tides in turn might lead to mass mortalities of both plankton, benthos and nekton (Burkholder *et al.*, 1992).

3 ORGANIC INPUTS IN THE MEDITERRANEAN: A COMPARISON BETWEEN THE EASTERN *VS.* WESTERN BASIN

The comparison proposed in this study takes into account two areas which are assumed to represent the general characteristics of the Eastern and Western basin and that allow to highlight the differences between the two systems: the Cretan basin and the Algero-Provençal basin.

The Cretan basin can be characterised as a back-arc basin, relative to the Hellenic Trench. It is an area of recent tectonism dominated by the subduction of the African Plate below the Eurasia Plate. The Cretan basin is characterised by a very narrow and steep continental shelf (gradient 1.5°), while deeper parts of the Cretan basin (>1700-m depth) display relatively low gradients. The general SE flow is characterised by current speed ranging from 1.1 to $27\,cm\,sec^{-1}$ with highest values in summer that might cause sediment resuspension. Modified Atlantic waters (MAW) characterise the surface layer of the water column (down to about 75 m depth); below this depth the Cretan intermediate waters (CIW) and the Transitional Mediterranean Water (TMW, 300–600 m depth).

The Gulf of Lions, the Catalan Sea and part of the Algero-Provençal basin here considered as representative of the Western Mediterranean. The area is characterised by large continental shelves (60 to 120 km wide) facing the Gulf of Lions and the Ebro river, whereas a narrow shelf characterised the Balearic Islands (<20 km) and displays the presence of large canyons particularly developed in the Gulf of Lions. The Ebro slope and Catalan margin are characterised by short gully-type canyons, whereas no canyons *sensu stricto* have been observed in the northern margin of Mallorca and Minorca. Cyclonic regional circulation which represent the major dynamical factor along its slopes. All margins are swept by the Algero-Provençal current. Two segment margins (Perpignan and Barcelona) export large quantities of particulate matter with a dominant lithogenic character.

The trophic characteristics of the two areas, which apparently affect pelagic–benthic coupling processes, can be summarised as follow: The Western Mediterranean (especially in the Gulf of Lions) displays relatively high primary production values ($140\text{–}160\,mg\,C\,m^{-2}\,d^{-1}$) and about 90% of this production is utilised before reaching the sea floor (Conan *et al.*, 1996). By contrast, the Eastern Mediterranean (and particularly the Cretan Sea) is the most oligotrophic area of the Mediterranean (Dugdale and Wilkerson, 1988), resembling trophic condition reported for the Sargasso Sea. In the Cretan sea primary production estimates range between $\approx 19\text{–}60\,mg\,C\,m^{-2}\,d^{-1}$, and about 97–98% of the exported production is mineralised before reaching the sediments. In the Cretan Sea mass fluxes ($0.21\,g\,m^{-2}\,d^{-1}$) are much lower than in the NW-Mediterranean where mass fluxes might reach $50\,g\,m^{-2}\,d^{-1}$ (Heussner *et al.*, 1990). Mass fluxes are generally spatially quite variable (for instance fluxes in the canyons are at least double than those measured in the open slope). The ratio of the mass fluxes in the two basins at the same depth might vary from 1 (when comparing

Baleares with the Cretan Sea), to 81 in the case of the comparison of Barcelona canyon head *vs*. Cretan Sea slope. The difference between the two areas becomes even more evident when comparing the organic carbon, carbohydrates and proteins fluxes: values from the Western Mediterranean are 1 to 2 orders of magnitude higher than those reported for the Cretan Sea. This was reflected also in terms of quality of the nutrient inputs to the benthos (expressed as labile organic matter contribution to the total mass flux): 1–8 *vs*. 0.8% in the Western Mediterranean and Cretan Sea, respectively (Buscail *et al.*, 1990; Danovaro *et al.*, 1999). Sedimentary parameters reflected this pattern. The concentrations of organic carbon in surface sediments in the two areas reflected the difference in OC flux (0.30–0.67% in the Cretan Sea *vs.* 0.69–0.94% in the W-Mediterranean. The biochemical composition of the sedimentary organic matter of the Cretan Sea revealed a rather poor quality (Danovaro *et al.*, 1993). Carbohydrates, being the dominant biochemical component, were mostly composed of refractory compounds. By contrast, sedimentary OM in the NW-Mediterranean was of much higher quality with proteins as the dominant fraction of the biodegradable material.

Bacterial densities at equally deep sediments are generally about double in the Western basin (Delille *et al.*, 1990) and meiofaunal abundance in the Cretan Sea is 4 to 25 times lower than that in the North-Western Mediterranean (*viz*. 60–120 *vs*. 500–1500 ind./10 cm^2, respectively; Soetaert *et al.*, 1991; Dinet and Vivier, 1977).

Benthic communities inhabiting shallow water depths are closely coupled to seasonal changes in food supply. Data from Western and Eastern basins enabled us to compare benthic responses to the varying food inputs in the two areas. In the NW-Mediterranean, a strong coupling between pelagic processes and benthic response can be detected. By contrast, in the Cretan deep basin there was an apparent lack of response to the seasonally varying food inputs.

Bacteria and meiofauna represent, quantitatively, the two most important benthic components in the deep sea, providing important indications on the structure and functioning of deep-sea ecosystems. At about 1000-m depth in the Lacaze-Duthiers canyon (NW-Mediterranean) bacteria represented only about 50% of the total benthic biomass whereas at about 1000-m depth in the Cretan Sea bacteria accounted for about 95% of the total benthic biomass. This indicates that benthic biomass of the Cretan Sea is more dominated by bacteria than in equally deep benthic sites of the Western Mediterranean. Since organic matter displays higher refractory composition with increasing depth, it is likely that the increase in bacterial dominance with depth is due to the ability of bacteria to exploit refractory compounds not directly available to meiobenthos. Thus bacteria in deep-sea sediments may play a primary role as trophic reservoir converting refractory compounds into available food (*i.e.* bacterial biomass).

The lack of significant seasonal changes in Cretan Sea deep-sea benthos might suggest that the supply and or the quality of organic matter below 500 m is not strong enough to support a density or biomass increase (Tselepides and Eleftheriou, 1992). The resulting competition for energy repartition between bacteria and metazoans for labile resources is likely to determine the prevalence of the microbial components. This supposition is supported by the observation that when bacteria are subdominant or slightly dominant (about 50% of the total biomass in the continental shelf and slope until 500 m depth), meiofauna still react (*e.g.* with increased copepod densities) to nutrient inputs. By contrast when bacteria account for 90% or more of the total benthic biomass, meiofaunal density did not react to nutrient inputs. The strong bacterial dominance in the Eastern Mediterranean suggests that the major part of the carbon flow was channelled through the bacteria. This fact is clearly in contrast with the scenario observed in the Western Mediterranean where at depth around 1000-m, the bacterial biomass represents less than 50% of the total benthic biomass. Higher quantity and quality of organic nutrient supply in the Western basin enable detritivores to get immediate benefit, rapidly increasing in number. This result in significantly higher meiofaunal densities and the clear response to organic carbon fluxes.

4 EFFICIENCY OF THE MEDITERRANEAN ECOSYSTEMS IN EXPLOITING ORGANIC INPUTS

Pelagic-benthic coupling in terms of gross composition of the living biomass is difficult to demonstrate (Grebmeier *et al.*, 1988; Grebmeier and McRoy, 1989). The quality and quantity of food arriving at the benthos are supposed to be important in determining the body composition of benthic organisms but have received little attention (Gallagher and Ambrose, 1998). Recent studies have suggested the presence of a strong pelagic–benthic coupling between water column processes and biochemical composition of the benthic fauna (Ambrose and Renaud, 1995; Graeve *et al.*, 1997). The main conclusion of these studies is that the composition and availability of the food sources is likely to influence also the biochemical composition of the benthic species. Such findings implement previous studies on both plankton (Bamstedt, 1978; Hopkins *et al.*, 1993) and benthic organisms (Lehtonen, 1996; Miliou *et al.*, 1992) that emphasised the influence of seasonal fluctuations in physical (*e.g.* temperature) and biological constraints on the biochemical compositions, energy content and calorific value of marine invertebrates (Falk-Petersen, 1981; Lehtonen, 1996).

The varying biochemical composition (particularly in terms of protein and lipid level) is generally assumed to be the result of different bioenergetic strategies in populations inhabiting different environments (Lehtonen, 1996).

Different trophic conditions (as those reported in the Eastern and NW Mediterranean) are likely to induce different bioenergetic strategies. In other words we should try to answer to the following questions: (1) are there different bioenergetic strategies in the two basins? and (2) which bioenergetic strategies have been adopted to cope with the extremely oligotrophic and unpredictable food inputs in the Eastern Mediterranean?

Lipid accumulation is the most widespread long-term energy storage strategy in aquatic crustaceans and their reproductive potential is largely dictated by lipid content (Sargent and Henderson, 1986). A comparative study carried out on biochemical composition of nematodes (the dominant metazoan taxon of deep-sea benthos) from the Eastern and Western basin reported significantly higher lipid concentrations in deep-sea specimens from the Eastern Mediterranean (Danovaro *et al.*, 1999a). Deep-sea benthic organisms from regions characterised by highly variable food inputs must have efficient energy storage systems to be able to cope with long periods of very low food availability (Sargent and Whittle, 1981). The differences in lipid level between nematodes from the two study areas of the Mediterranean might be explained with the need to accumulate, opportunistically, lipids during short periods of food availability to be able to survive to long periods of indigence. Bioenergetic strategies similar to those reported above have been reported for deposit-feeding amphipods and other deep-sea species living at high latitudes which are known to be characterised by high temporal variability with short periods of extremely large food availability (*e.g.* in the Arctic; Clarke, 1983; Sargent and Henderson, 1986). Therefore, it is possible that the unpredictability of the food nourishment rather than the oligotrophy of the environment could determine the bioenergetic strategy of the benthic components.

The extreme oligotrophy of certain systems has been demonstrated to play an important role in the community structure and, for instance can result in a diminished average size of the benthic organisms. The combined effects of food limitation and temporal variability in food supply might have important implication for bioenergetic strategies at ecosystem level. In the deep Cretan Sea a close coupling has been observed between particle fluxes, sedimentary organic matter composition and concentration, individual nematode energy content and biomass (Danovaro *et al.*, 1999a). Calculations of the energy content of nematodes suggest an apparent balance between diminished size and increased energy content (in terms of lipid storage) has a possible mechanism to optimise resource partitioning and exploitation.

In order to define the efficiency of the benthic metazoans in exploiting the available organic matter inputs from the photic layers, ratios between organic carbon fluxes and the number of organisms supported by the food input were calculated. As reported above meiofaunal densities in the NW-Mediterranean are higher than in the Cretan Sea but each meiofaunal organism in the NW-Mediterranean has a larger nutrient availability. For instance, about $0.14\,\mathrm{mg\,C\,ind.}^{-1}$ of meiofauna are fuelled daily in the Western Mediterranean compared to the $0.07\,\mathrm{mg\,C\,ind.}^{-1}$ of the Eastern Mediterranean. The same applies to bacteria. The ratio between organic carbon fluxes and bacterial biomass indicates that 3.3 mg C were provided daily per 1 mg C of bacterial biomass in the Western Mediterranean, compared to 0.07 in the Eastern Mediterranean. These data, confirm that quantitative differences between the two areas are related to the different organic carbon inputs from the photic layer but also allow to infer about the efficiency of the deep-sea ecosystems of the two basins in exploiting the nutrient inputs. In fact, if we hypothesise that a ratio of $0.14\,\mathrm{mg\,C\,ind.}^{-1}$ is required by meiofauna in the NW-Mediterranean but meiofauna from the Western basin would receive the organic carbon fluxes of the Eastern Mediterranean, the meiofauna would be so much nutrient limited to be reduced to be about half of those observed. With a similar approach it might be estimated that bacterial biomass in the NW-Mediterranean in the scenario of food limiting conditions would be 50 times lower. Data for meiofaunal comparison at biomass level are not available but calculation based on bacterial biomass reported above would suggest a significant functional difference (Danovaro *et al.*, 1999b).

5 EFFECTS OF CLIMATE CHANGES ON TROPHIC STATE OF THE DEEP-EASTERN MEDITERRANEAN

Climate changes are expected to determine strong modifications in the structure and functioning of ecosystems (Hayward, 1997). Recent studies carried out in the south Aegean Sea in the last decade proved the formation, induced by climate anomalies, new water masses altering the steady state hydrological conditions (Roether *et al.*, 1995). Two main hydrological changes were observed: the first occurred within the period 1987–1992, when a massive production of a new water mass characterised by high temperatures, salinity and dissolved oxygen (Cretan Dense Water), gradually filled the Cretan Sea. The second anomaly occurred from 1992 to 1994, when bottom waters (at depths >1500 m) experienced a significant drop of temperature (of about 0.4 °C; Theocharis *et al.*, 1993). These new colder water masses rapidly replaced the previous deep waters with a consequent uplift of nutrient rich waters into the euphotic layer. Such upwelling induced as expected an enhanced primary production and presumably increased *f*-ratio. From literature data it seems that between early 1980s and 1995 (Dugdale and Wilkerson, 1988; Psarra *et al.*, 1995) primary production almost triplicated (60–$80\,\mathrm{g\,C\,m}^{-2}\,\mathrm{y}^{-1}$) so that differences between the Algero-Provençal and Cretan basin might have been notably reduced. The increased primary production was reflected increased input of primary organic matter to the bottom (Danovaro *et al.*, 1998b). As a consequence sediments accumulated organic compounds such as proteins, which were less utilised as a result of the decreased temperatures and consequent reduced bacterial activity (Danovaro *et al.*, 2002). These data support the hypothesis that climate changes might have rapid and profound effects on pelagic–benthic coupling and carbon cycling in deep-sea ecosystems.

References

Ambrose, W. G. and Renaud, P. E. (1995). Benthic response to water column productivity patterns: Evidence for benthic–pelagic coupling in the northeast Water Polynya. *Journal of Geophysical Research*, **110**, 4411–4421.

Bamstedt, U. (1978). Studies on the deep-water pelagic community of Korsfjorden, western Norway: Seasonal variation in weight and biochemical composition of *Chiridius armatus* (Copepoda), *Boreomysis arctica* (Mysidacae), and *Eukrohnia hamata* (Chaetognatha) in relation to their biology. *Sarsia*, **63**, 145–154.

Boero, F., Belmonte, G., Fanelli, G., Piraino, S. and Rubino, F. (1996). The continuity of living matter and the discontinuities of its constituents: Do plankton and benthos really exist? *Trends in Ecology & Evolution*, **11**, 177–180.

Burkholder, J. M., Noga, E. J., Hobbs, C. H. and Glasgow, H. B. (1992). New "phantom" dinoflagellate is causive agent of major estuarine fish kills. *Nature*, **358**, 407–410.

Buscail, R., Pocklington, R., Daumas, R. and Guidi, L. (1990). Fluxes and budget of organic matter in the benthic boundary layer over the north western Mediterranean margin. *Continental Shelf Research*, **10**, 1089–1122.

Clarke, A. (1983). Life in cold water: The physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Ann. Rev.*, **21**, 341–453.

Conan, P., Leveau, M. and Raimbault, P. (1996). EUROMARGE-NB Production primaire et flux des élements, in Canals, M., Casamor, J. L., Calafat, A. M. and Monaco, A. (eds.), *EUROMARGE final report.* MAST II Programme, EC; Vol. III.

Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A. and Tselepides, A. (2001). Deep-sea ecosystem response to climate changes: The Eastern Mediterranean case study. *Trends in Ecology & Evolution*, **16**, 505–510.

Danovaro, R., Dell'Anno, A., Martorano, D., Parodi, P., Marrale, D. and Fabiano, M. (1999a). Seasonal changes in the biochemical composition of deep-sea nematodes: Bioenergetic and methodological considerations. *Marine Ecology-Progress Series*, **179**, 273–283.

Danovaro, R., Della Croce, N., Dell'Anno, A., Fabiano, M., Marrale, D., Parodi, P., Theocharis, A. and Tselepides, A. (1998b). Long-term changes in deep-sea benthic ecosystems: The eastern Mediterranean case. *3rd MTP-II-MATER workshop on the variability of the Mediterranean Sea*, pp. 202–203.

Danovaro, R., Della Croce, N., Eleftheriou, A., Fabiano, M., Papadopoulou, N., Smith, C. and Tselepides, A. (1995). Meiofauna of the deep E-Mediterranean Sea: Distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. *Progress in Oceanography*, **36**, 329–341.

Danovaro, R., Dinet, A., Duineveld, G. and Tselepides, A. (1999b). Benthic response to particulate fluxes in different tropic environments: A comparison between the western and eastern Mediterranean. *Progress in Oceanography*, **44**, 287–312.

Danovaro, R., Fabiano, M. and Della Croce, N. (1993). Labile organic matter and microbial biomasses in deep sea sediments (eastern Mediterranean Sea). *Deep-Sea Research*, **40**, 953–965.

Danovaro, R., Marrale, D., Della Croce, N., Dell'Anno, A. and Fabiano, M. (1998a). Heterotrophic nanoflagellates, bacteria and labile organic compounds in continental shelf and deep-sea sediments of the eastern Mediterranean. *Microbial Ecology*, **35**, 244–255.

Delille, D., Guidi, L. D. and Cahet, G. (1990). Temporal variations of benthic bacterial microflora on the north western Mediterranean continental shelf and slope. *Marine Ecology*, **11**, 105–115.

Deming, J. W. and Yager, P. L. (1992). Natural bacterial assemblages in deep-sea sediments: Toward a global view, in Rowe, G. T. and Pariente, V. (eds.), *Deep-sea food chains and the global carbon cycle.* Kluwer Academic Publisher, pp. 11–28.

Dinet, A. and Vivier, M. H. (1977). Le meiobenthos abyssal du Golf de Gascogne I. Considerations sur les donnés quantitatives. *Cahiers de Biologie Marine*, **18**, 85–97.

Dugdale, R. C. and Wilkerson, F. R. (1988). Nutrient sources and primary production in the eastern Mediterranean. *Oceanologica Acta*, **9**, 178–184.

Falk-Petersen, S. (1981). Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: Seasonal changes in body weight and the main biochemical composition of *Thysanoessa inermis* (Krøyer), T. *raschi* (M. Sars), and *Meganyctiphanes norvegica* (M. Sars) in relation to environmental factors. *J. Exp. Mar. Biol. Ecol.*, **49**, 103–120.

Gallagher, M. L. and Ambrose, W. G. (1998). Comparative studies in biochemical composition of benthic invertebrates (bivalves, ophiuroids) from the northeast Water (NEW) Polynya. *Polar Biology*, **19**, 167–171.

Gooday, A. J. and Turley, C. M. (1990). Response by benthic organisms to input of organic material to the ocean floor. *Philosophical Transactions of the Royal Society of London*, **331**, 119–138.

Gooday, A. J., Pfannkuche, O. and Lambshead, P. J. D. (1996). Apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic. *J. Mar. Biol. Ass. UK*, **76**, 297–310.

Graeve, M., Kattner, G. and Piependurgo, D. (1997). Lipids in Arctic benthos: Does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biology*, **18**, 53–61.

Graf, G. (1989). Benthic-pelagic coupling in a deep-sea benthic community. *Nature (London)*, **341**, 437–439.

Grebmeier, J. M. and McRoy, C. P. (1989). Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. *Marine Ecology Progress Series*, **53**, 79–91.

Grebmeier, J. M., McRoy, C. P. and Feder, H. M. (1988). Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I Food supply source and benthic biomass. *Marine Ecology Progress Series*, **48**, 57–67.

Hairston, N. G., Ellner, S., Jr. and Kearns, C. M. (1996). Overlapping generations: The storage effect and the maintenance of biotic diversity, in Rhodes, O. E., Chesser, R. K., Jr. and Smith, M. H. (eds.), *Population dynamics in ecological space and time*, Univ. Chicago Press.

Hayward, T. L. (1997). Pacific Ocean climate change: Atmospheric forcing, ocean circulation and ecosystem response. *Trends in Ecology & Evolution*, **12**, 150–154.

Heussner, S., Ratti, C. and Carbonne, J. (1990). The PPS 3 time-series sediment trap and the sample processing technique used during the ECOMARGE experiment. *Continental Shelf Research*, **10**, 943–958.

Hopkins, C. C. E., Sargent, J. R. and Nilssen, E. M. (1993). Total lipid content, and lipid and fatty acid composition of the deep-water prawn Pandalus borealis from Balsjord, northern Norway: Growth and feeding relationships. *Marine Ecology Progress Series*, **96**, 217–228.

Kemp, P. F. (1994). Microbial carbon utilization on the continental shelf and slope during the SEEP-II experiment. *Deep-Sea Research*, **41**, 563–581.

Lehtonen, K. K. (1996). Ecophysiology of the benthic amphipod Monoporeia affinis in an open-sea area of the northern Baltic Sea: Seasonal variations in body composition, with bioenergetic considerations *Marine Ecology Progress Series*, **143**, 87–98.

Marcus, N. H. and Boero, F. (1998). The importance of benthic–pelagic coupling and the forgotten role of the life cycles in coastal aquatic ecosystems. *Limnology and Oceanography*, **43**, 23–28.

Marcus, N. H., Lutz, R. V., Burnett, W. and Cable, P. (1994). Age, viability and vertical distribution of zooplankton resting eggs from an anoxic basin: Evidence of an egg bank. *Limnology and Oceanography*, **39**, 763–768.

Miliou, H., Moraitou-Apostopoulu, M. and Argyridou, M. (1992). Biochemical composition of Tisbe holothuriae (Copepoda: Harpacticoida) and its differentiation in relation to developmental stages. *Ophelia*, **36**, 159–166.

Pfannkuche, O. (1992). Organic carbon through the benthic community in the temperate abyssal NE-Atlantic, in Rowe, G. T. and Pariente, V. (eds.), *Deep-sea food chains and the global carbon cycle.* Kluwer Academic Publisher, Dordrecht, pp. 183–197.

Pfannkuche, O. (1993). Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47°N, 20°W. *Deep-Sea Research*, **40**, 135–149.

Pfannkuche, O. and Lochte, K. (1993). Open ocean pelagic–benthic coupling: Cyanobacteria as tracers of sedimenting salp faeces. *Deep-Sea Research*, **40**, 727–737.

Pfannkuche, O. and Thiel, H. (1987). Meiobenthic stocks and benthic activity on the NE-Svalbard shelf and in the Nansen basin. *Polar Biology*, **7**, 253–266.

Pfannkuche, O., Beckman, W., Christiansen, B., Lochte, K., Rheinheimer, G., Thiel, H. and Weikert, H. (1990). BIOTRANS, Biologisches vertikaltransport und energiehaushault in der bodennahen Wasserschicht der Tiefsee. Berichte aus dem Zentrum für Meeres-und Klimaforschung der Universität Hamburg, Vol. 10, p. 159.

Psarra, S., Tselepides, A., Ignatiades, L. and Dafnomili, E. (1996). Primary production estimates in the Cretan Sea, in Tselepides, A., Papadopoulou, K.-N. and Polychronaki, T. (eds.), *CINCS: Pelagic–benthic coupling in the oligotrophic Cretan sea.* Mediterranean Targeted Project, *Final Report MAST II*, pp. 46–52.

Rice, A. L., Thurston, M. H. and Bett, B. J. (1994). The IOSDL DEEPSEAS programme: Introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting abyssal sites in the north-eastern Atlantic. *Deep-Sea Research*, **41**, 1305–1320.

Roether, W., Manca, B., Klin, B., Bregant, D., Geogopoulos, D., Beitzel, V., Kovacevic, V. and Luchetta, A. (1996). Recent changes in eastern Mediterranean deep waters. *Science*, **271**, 333–335.

Rowe, G. T. (1983). Biomass and production of deep-sea macrobenthos, in Rowe, G. (ed.), *Deep-sea biology.* Wiley Interscience, New York, pp. 97–121.

Rowe, G. T., Sibuet, M., Deming, J., Tietjen, J. and Khripounoff, A. (1990). Organic carbon turnover time in deep-sea benthos. *Progress in Oceanography*, **24**, 141–160.

Sargent, J. R. and Henderson, R. J. (1986). Lipids, in Corner, E. D. S. and O'Hara, S. C. M. (eds.), *The biological chemistry of marine copepods.* Clarendon Press, Oxford, pp. 59–108.

Sargent, J. R. and Whittle, K. (1981). Lipids and hydrocarbons in the marine food web, in Longhurst, A. R. (ed.), *Analysis of marine ecosystems.* Academic Press, London, pp. 491–533.

Soetaert, K., Heip, C. and Vincx, M. (1991). The meiobenthos along a Mediterranean deep-sea transect off Calvi (Corsica) and in an adjacent canyon. *PSZNI: Marine Ecology*, **12**, 227–242.

Theocharis, A., Georgopoulos, D., Lascaratos, A. and Nittis, K. (1993). Water masses and circulation in the central region of the eastern Mediterranean: Eastern Ionian, south Aegean and northwest Levantine, 1986–1987. *Deep-Sea Research*, **40**, 1132–1142.

Thiel, H. (1983). Meiobenthos and nanobenthos of the deep sea, in Rowe, G. (ed.), *Deep-sea biology.* Wiley, New York, pp. 167–230.

Tietjen, J. H. (1992). Abundance and biomass of metazoan meiobenthos in the deep sea, in Rowe, G. T. and Pariente, V. (eds.), *Deep-sea food chains and the global carbon cycle.* Kluwer Academics Publishers, pp. 45–62.

Tselepides, A. and Eleftheriou, A. (1992). south Aegean (eastern Mediterranean) continental slope benthos: Macroinfaunal-environmental relationships, in Rowe, G. T. and Pariente, V. (eds.), *Deep-sea food chains and the global carbon cycle.* Kluwer Academics Publishers, pp. 139–156.

Wassmann, P., Andreassen, I., Reigstad, M. and Slagstd, D. (1996). Pelagic–benthic coupling in the Nordic Seas: The role of episodic events. *PSZNI: Marine Ecology*, **17**, 447–471.