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Review

Biological Responses to Seasonally Varying Fluxes of Organic Matter to the Ocean Floor: A Review

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Deep-sea benthic ecosystems are sustained largely by organic matter settling from the euphotic zone. These fluxes usually have a more or less well-defined seasonal component, often with two peaks, one in spring/early summer, the other later in the year. Long time-series datasets suggest that inter-annual variability in the intensity, timing and composition of flux maxima is normal. The settling material may form a deposit of "phytodetritus" on the deep-seafloor. These deposits, which are most common in temperate and high latitude regions, particularly the North Atlantic, evoke a response by the benthic biota. Much of our knowledge of these responses comes from a few time-series programmes, which suggest that the nature of the response varies in different oceanographic settings. In particular, there are contrasts between seasonal processes in oligotrophic, central oceanic areas and those along eutrophic continental margins. In the former, it is mainly "small organisms" (bacteria and protozoans) that respond to pulsed inputs. Initial responses are biochemical (e.g. secretion of bacterial exoenzymes) and any biomass increases are time lagged. Increased metabolic activity of small organisms probably leads to seasonal fluctuations in sediment community oxygen consumption, reported mainly in the North Pacific. Metazoan meiofauna are generally less responsive than protozoans (foraminifera), although seasonal increases in abundance and body size have been reported. Measurable population responses by macrofauna and megafauna are less common and confined largely to continental margins. In addition, seasonally synchronised reproduction and larval settlement occur in some larger animals, again mainly in continental margin settings. Although seasonal benthic responses to pulsed food inputs are apparently widespread on the ocean floor, they are not ubiquitous. Most deep-sea species are not seasonal breeders and there are probably large areas, particularly at abyssal depths, where biological process rates are fairly uniform over time. As with other aspects of deep-sea ecology, temporal processes cannot be encapsulated by a single paradigm. Further long time-series studies are needed to understand better the nature and extent of seasonality in deep-sea benthic ecosystems.

Keywords:
· Deep-sea benthos,
· phytodetritus,
· fluxes,
· seasonality,
· bacteria,
· foraminifera,
· meiofauna,
· macrofauna,
· megafauna,
· reproduction.

1. Introduction

Seasonality is an important feature of littoral and sublittoral benthic ecosystems (e.g. Graf, 1992; Barnes and Clarke, 1995; Coma *et al.*, 2000). In a much-quoted passage, Moseley (1880) ventured the opinion that a "periodic variation in the supply of food falling from above ... may give rise to a little annual excitement amongst the inhabitants" of the deep sea. For much of the 20th century, however, this remote environment was generally believed to be buffered from seasonality by the overlying water column (Menzies, 1965). In terms of its physicochemical characteristics, the deep sea is certainly more stable, generally, than continental shelf and coastal environments. Yet its stability is only relative, and in many respects the ocean floor does not conform to this paradigm (Tyler, 1996). On geological time scales, the history of the oceans has been punctuated by major events that have changed the characteristics of the benthic envi-

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Table 1. Deep-sea programmes addressing some aspect of benthopelagic coupling.

Site/Project	Period of study	Location and water depth (m)	Measurements and faunal components	Environmental characteristics	Key references
BIOTRANS Area	1984–1999	NE Atlantic: 47°N, 20°W; 4550 m	SCOC, phytodetritus deposits, pigments, biochemical activity, bacteria, metazoan meio-macro-fauna	Well-oxygenated, abyssal open ocean site with seasonal phytodetritus deposition	Lochte (1992); Pfannkuche (1993)
EU/BENGAL Site	1989–1998	NE Atlantic, Porcupine Abyssal Plain: 48°50′ N, 16° 30′ W; 4850 m	Time-lapse photography, phytodetritus deposits, pigments, foraminifera, metazoan meio-, macro-mega-fauna	Well-oxygenated, abyssal open ocean site with seasonal phytodetritus deposition	Rice *et al.* (1994, 1998); Billett and Rice (2001)
Goban Spur	OMEX I 1993–1996; OMEX II, 1996–1999	NE Atlantic: 47–50°N, 7–14°W	Fluxes, currents; phytodetritus deposits, SCOC, small organism and macrofaunal responses	Well-oxygenated continental margin with shelf-edge upwelling; sediments range from sands to hemipelagic clayey silts	van Weering *et al.* (1998)
Rockall Trough Permanent Station	1973–	NE Atlantic: 54°40′ N, 12°16′ W; 2900 m	Epibenthic sledge samples for studies of macro- and mega-faunal population dynamics and reproduction	Well-oxygenated continental margin; Globigerina ooze, organic carbon 0.47%	Gage *et al.* (1980)
ECOFER	1987–1991	NE Atlantic, Bay of Biscay: 44–45°N, 2–4°W; down to 3000 m	Time-series sediment trap moorings; sampling of "suprabenthos" using epibenthic sledge	Continental margin cut by canyons; no strong seasonal signal in vertical particle flux; bottom-water temperatures ~3°C	Monaco *et al.* (1999)
ECOMARGE	1984–1988	NW Mediterranean margin, Gulf of Lions	Water-column sampling, nephelometry; sediment traps; box-cores for metazoan meiofauna and geochemistry; megafaunal reproduction	Continental margin cut by canyons; high seasonal flux variability; bottom-water temperatures ~13°C	Monaco *et al.* (1990)
DYFAMED-BENTHOS	1993–1997	NE Mediterranean, Ligurian Sea: 43°24.6′ N, 7°51.7′ W; 2300 m	Maxicorer samples for metazoan meiofauna	Seasonal variations in partical flux; bottom-water temperature >12.8°C	Gehlen *et al.* (1997); Guidi-Guilvard *et al.* (2000) Guidi-Guilvard (2002)
CINCS project	May 1994 to June 1996	E. Mediterranean, Cretan Sea: 35–36°N, 24°30′–25°30′ E; shelf to >1500 m	Primary production, fluxes, SCOC, pigments, bacteria, flagellates, meio- macro- mega-fauna	Highly oligotrophic area; bottom-water temperature >12.8°C	Tselepides & Polychronaki (2000)
Station M	1989–1996	NE Pacific: 34°50′ N, 123°00′ W; 4100 m	Fluxes, water-column sampling; currents; pigments; C_{org}; phytodetritus; SCOC, macro-mega-fauna; submersible observations; time-lapse photography	Relatively eutrophic abyssal site located beneath California current; sediment a silty clay	Druffel & Smith (1998)
Stn SB, Sagami Bay	1989–1999	Off Japan: 35°00′ N, 139°22.9′ W; 1430 m	Primary productivity, fluxes, seafloor deposits, pigments, foraminifera, metazoan meiofauna	Eutrophic continental margin site in coastal embayment; O_2 = ~1 ml/l	Kitazato *et al.* (2000); Shimanaga *et al.* (2000); Shimanaga & Shirayama (2000)

ronment at regional and global scales. Many of these upheavals were linked to changes in thermohaline circulation associated with climatic shifts. Of greater immediate interest to biologists are events that occur on ecological time scales. During the 1970s and 1980s it emerged that the deep sea is subject to various disequilibrium processes that have a profound effect on the structure, composition and functioning of indigenous biological communities. These may be physical, chemical, or biological in nature and, for convenience, can be divided into two categories, unpredictable and predictable (Tyler *et al*., 1994; Tyler, 1996). It should be remembered, however, that this division is artificial since even "unpredictable" events will become predictable given a long enough time scale.

Unpredictable variations are caused by, in approximate order of intensity, catastrophic disturbance such as slumps, slides and turbidity current (Masson *et al*., 1996), the development of seeps and vents (Van Dover, 2000), benthic storms (Thistle *et al*., 1991), episodic resuspension and downslope transport of upper shelf sediments following increased river discharges caused by heavy rainfall (Gehlen *et al*., 1997), large food falls (Smith, 1986), and pulses of faecal pellets originating from swarms of pelagic animals such as salps (Graf, 1989; Pfannkuche and Lochte, 1993). Whale falls to the deep-seafloor, which one might think were entirely unpredictable, may have a seasonal component arising from migrations patterns (Smith *et al*., 1989). Other more or less predictable variations in the seafloor environment include El Niño oscillations (Arntz *et al*., 1991), annual variation in eddy kinetic energy (Dickson *et al*., 1982, 1986), semidiurnal tidal variation (Lampitt *et al*., 1983; Lampitt and Paterson, 1988), the possible delivery of macrophyte debris by seasonal storms (Menzies and Rowe, 1969; Turner, 1973; Wolff, 1979; Tyler, 1988, 1996) and seasonal phytodetritus inputs. Thus, seasonal phenomena are just one category of disequilibrium processes that have a potential impact on deep-sea benthic communities over time scales ranging from days to decades or longer. They are, however, of profound importance for understanding ecosystem functioning in the deep ocean, as well as the biogeochemical cycling of organic carbon and the generation of the palaeoceanographic record (Ducklow and Harris, 1993; Eglinton *et al*., 1995; Graf *et al*., 1995).

Earlier reviews have dealt with temporal fluctuation among the deep-sea benthos. Tyler (1988) summarised evidence for seasonal fluxes and biological processes in the deep sea; Gooday and Turley (1990) discussed the responses of benthic organisms and communities to different kinds of organic matter input, both predictable and unpredictable. Gooday and Rathburn (1999) reviewed the responses of benthic foraminifera to temporal disturbances. Since the papers of Tyler (1988) and Gooday and Turley (1990), there has been an explosion of literature addressing seasonal fluxes through the water column and deep-sea benthic responses. The present review is selective and addresses 1) evidence for seasonal fluxes of material through the water column and their arrival as phytodetrital deposits on the deep-seafloor and 2) benthic responses to these inputs. I start, however, by mentioning some important research programmes which have contributed to our understanding of this important topic.

2. Important Programmes

Seasonal changes in the deep sea can been detected by studying samples taken before and after pulses of organic matter. Seasonal cycles have been pieced together from samples taken during different years, an approach that is compromised by possible inter-annual variability. In order to more fully document and understand seasonal processes in the water column and on the seabed, it is necessary to conduct time series sampling over a period of several years. Because of financial and logistic constraints, however, relatively few time-series studies of water column fluxes and the benthic responses have been conducted in the deep sea. Those that have been carried out are summarised in Table 1. To a large extent, the data summarised in this review have been derived from these national and international programmes. There is a concentration of studies in the NE Atlantic and Mediterranean; two have been carried out in the North Pacific. Most study sites are located in continental margin settings easily accessible to research vessels; a few are in more open ocean, abyssal settings.

3. The Detection of Seasonal Signals in the Interior of the Ocean

3.1 Fluxes through the water column

Evidence for the transmission of a seasonal signal to the interior of the ocean first emerged during the late 1970s and 1980s from sediment trap records (e.g. Deuser and Ross, 1980; Honjo, 1982; Deuser, 1986). These early studies (reviewed by Tyler, 1988) were conducted at five different locations in the North Atlantic, northeast and eastern equatorial Pacific (Panama Basin). They established that distinct seasonal fluctuations occur in the total particulate flux and its components, and that these changes are related to cycles in primary productivity. They also demonstrated the existence of interannual variations in the magnitude and timing of the flux maxima. Subsequent investigations, combined with measurements of upper ocean primary productivity, have confirmed that temporal variations in surface productivity are transmitted down through the water column by particles sinking at rates of 100–200 m per day (Lampitt, 1985; Newton *et al*., 1994; Honjo *et al*., 1995; Baldwin *et al*., 1998; Nodder and Northcote, 2001). The penetration of organic matter fluxes into the interior of the ocean demonstrates that benthopelagic coupling can occur even at abyssal depths (Asper *et al.*, 1992). The large quantities of fresh (labile) organic matter sinking out of the upper mixed layer during these events may account for >50% of the total flux at a particular site (e.g. Honjo and Manganini, 1993; Newton *et al.*, 1994).

Seasonal changes in fluxes are reported from continental margin and open ocean, eutrophic and oligotrophic settings. These include seasonally ice-covered areas off NW Greenland where flux variations are particularly strong (Ramseier *et al.*, 1999), the temperate NE Atlantic (Honjo and Manganini, 1993; Newton *et al.*, 1994; Lampitt *et al.*, 2001), the eastern tropical Atlantic (Fischer and Wefer, 1996), the Gulf of Lions and Catalan Sea in the western Mediterranean where fluxes are influenced by the presence of canyons (Danavaro *et al.*, 1999), the Ligurian Sea, also in the western Mediterranean, where complex physical and biological processes regulate seasonal changes in flux intensity (Miquel *et al.*, 1994), the highly oligotrophic eastern Mediterranean off the north coast of Crete (Danavaro *et al.*, 2000a; Stavrakakis *et al.*, 2000), the highly eutrophic Arabian Sea (Nair *et al.*, 1989; Haake *et al.*, 1993; Honjo *et al.*, 1999; Rixen *et al.*, 2000), the Bay of Bengal (Ittekkot *et al.*, 1991), the Bering Sea and Subarctic Pacific (Wong *et al.*, 1999; Takahashi *et al.*, 2000), the central and eastern North Pacific (Smith and Baldwin, 1984; Smith, 1987), Station M off the Californian margin in the NE Pacific (Smith *et al.*, 1992, 1994; Baldwin *et al.*, 1998), the temperate SW Pacific (Nodder and Northcote, 2001) and off the Antarctic Peninsula where extreme seasonal variability is combined with low annual flux (Fischer *et al.*, 1988; Wefer and Fischer, 1991). Studies are concentrated in the Northern Hemisphere and the tropics; relatively few have been carried out south of the equator (Lampitt and Antia, 1997; Nodder and Northcote, 2001).

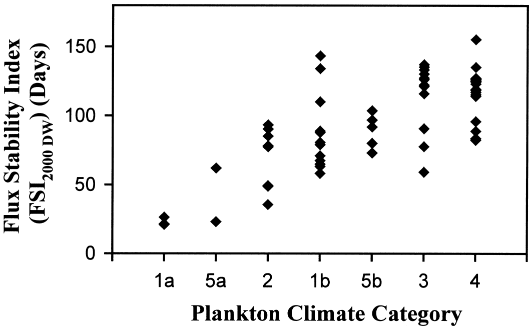

Fig. 1. Dry weight flux stability indices (FSI$_{DW2000}$) in relation to the upper ocean plankton provinces of Longhurst. Reprinted from *Deep-Sea Research I*, **44**, R. S. Lampitt and A. N. Antia, Particle flux in deep seas: regional characteristics and temporal variability, figure 12, p. 1397, © 1997 Elsevier Science Ltd, with permission from Elsevier Science.

Geographical patterns in the strength of seasonality in primary production influence the intensity of export production, i.e. the proportion of primary production that leaves the upper water column (Berger and Wefer, 1990). For example, seasonal flux variations are very pronounced in the western Arabian Sea (Honjo *et al.*, 1999) but weakly developed under the continuous upwelling area off Cap Blanc, NE Atlantic (Fischer and Wefer, 1996). Lampitt and Antia (1997) present a synoptic analysis of published trap records that document a full 12 month cycle. Following Berger and Wefer (1990), they determined a “Flux Stability Index” (FSI), defined as the time required for 50% of the total flux to be deposited during any particular year. FSI values increased with water depth in studies involving more than one trap, reflecting the transmission of seasonality into the ocean interior. Lampitt and Antia (1997) developed their analysis further by relating flux stability data to Longhurst’s (1995, 1998) system of upper ocean plankton provinces (Fig. 1). The five provinces (seven including subdivisions) for which data were available each had a characteristic FSI range (normalised to 2000 m water depth), although the provinces apparently had little influence on actual flux levels. Values of FSI$_{2000m}$ were highest in the tropics (i.e. these were the least seasonal regions) and lowest in the Antarctic (most strongly seasonal). This study confirms that a higher proportion of primary production is exported from the photic zone in temperate regions with a strong spring bloom than in tropical areas where production is more stable over time. Seasonal signals to the benthos are also weak in oligotrophic areas where most primary production is carried by small cells with slow sinking rates and organic production is recycled within complex microbial food webs (Legendre and Le Fèvre, 1995). In addition to these large-scale patterns, variations in flux intensity occur at smaller spatial scales, for example in relation to major frontal systems. Fluxes were higher and more strongly seasonal between summer 1996 and spring 1997 at a site north of the Subtropical Front (SW Pacific) compared to a site <200 km away to the south of the Front (Nodder and Northcote, 2001).

Export fluxes often reflect general patterns of primary production, although there are exceptions (e.g. Karl *et al.*, 1996) and other biological and physical factors also play a role in determining flux intensities (e.g. Miquel *et al.*, 1994; Boyd and Newton, 1995). In the Sargasso Sea, unimodal variations in flux intensity correspond to the annual cycle of surface phytoplankton production (Deuser, 1986; Deuser *et al.*, 1995). Other investigations have revealed more complex intra-annular patterns, often with a

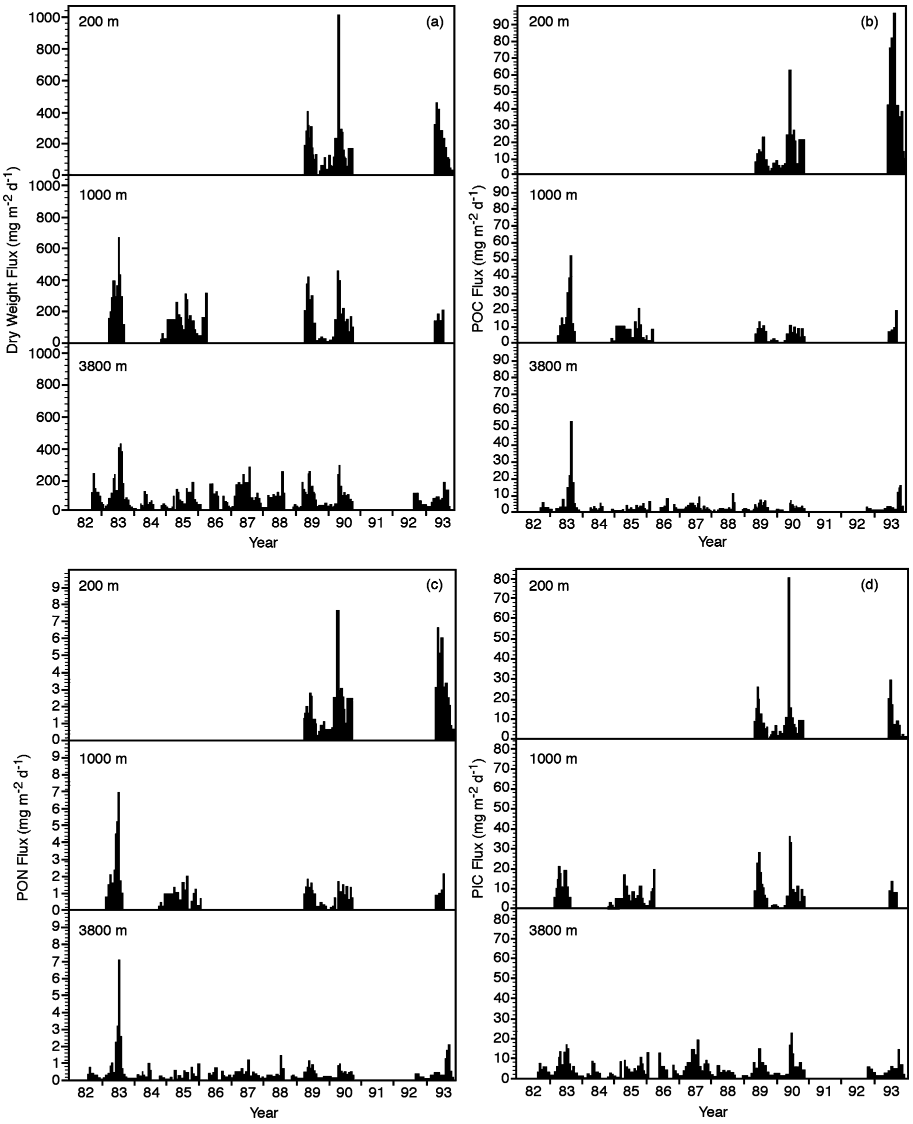

Fig. 2. Particle flux of a) mass as dry weight, b) particulate organic carbon, c) particulate organic nitrogen, d) particulate inorganic carbon, e) biogenic silica into sediment traps moored at water depths of 200 m, 1000 m and 3800 m at Ocean Station Papa (50°N, 145°W; water depth 4240 m) in the NE Pacific Ocean. Reprinted from *Deep-Sea Research II*, **46**, C. S. Wong, F. A. Whitney, D. W. Crawford, K. Iseki, R. J. Matear, W. K. Johnson, J. S. Page and D. Timothy, Seasonal and interannual variability in particle fluxes of carbon, nitrogen and silicon from time series sediment traps at Ocean Station P, 1982–1993: relationship to changes in subarctic primary productivity. p. 2741, figure 1, © 1999 Elsevier Science Ltd, with permission from Elsevier Science.

peak in the spring/early summer and another one later in the year. At a site in the Panama Basin, there was evidence for a bimodal pattern in POC (particulate organic carbon) flux that mirrored surface primary production (Honjo, 1982). At the NE Atlantic JGOFS site (47°N, 20°W), major spring and autumn peaks in fluxes of particulate inorganic carbon (PIN), POC and opal were evident in traps deployed at water depths of 3100 m and 4465 m (90 m above seafloor) during 1989 and 1990 (Newton *et al.*, 1994). At Station M in the NE Pacific, particulate fluxes at 600 mab and 50 mab were low in winter and there was a series of peaks concentrated in early summer and autumn (Smith *et al.*, 1992, 1994; Baldwin *et al.*, 1998). Short duration events characterised by fluxes, which are much higher than the seasonal average, are reported in some regions. In the subarctic North Pacific, high mass flux events were related to swarms of settling pteropods (Wong *et al.*, 1999). Rapidly sedimenting faeces originating from salp swarms can also generate unusually high flux rates (Bathmann, 1988;

Pfannkuche and Lochte, 1993).

In a general sense, seasonal flux patterns are usually fairly consistent between years (Deuser, 1986). There is growing evidence, however, for significant interannual variations in the timing and intensity of flux maxima, and the composition of the settling material (e.g. Deuser, 1986; Takahashi *et al*., 1989, 2000; Haake *et al*., 1993; Newton *et al*., 1994; Deuser *et al*., 1995; Baldwin *et al*., 1998; Wong *et al*., 1999; Lampitt *et al*., 2001) (Fig. 2). In seasonally ice-covered areas off NW Greenland, flux intensity varies from year to year in relation to the duration and magnitude of ice cover (Ramseier *et al*., 1999). In the Arabian Sea, inter- and intra-annular variations in primary production and organic-carbon flux intensity are closely linked to the strength of the monsoon and to changes in the geographical areas most strongly impacted by monsoon-generated wind stress (Haake *et al*., 1993; Honjo *et al*., 1999). According to Rixen *et al*. (2000), the strength of the low-level atmospheric jet (Findlater Jet) associated with the SW monsoon is the crucial factor determining upwelling intensity and therefore organic carbon fluxes in the western Arabian Sea. In the Bay of Bengal, on the other side of the Indian subcontinent, peaks in particle fluxes coincide with maximum river discharges during the SW monsoon period (Ittekot *et al*., 1991). Differences in the functioning of pelagic communities (i.e. the efficiency of the "biological pump"), rather than primary productivity, may also lead to interannular changes in export production and flux. At the NE Atlantic JGOFS site, the first 1989 flux event was characterised by diatoms derived from the spring bloom, the second by sticky gelatinous material composed of muccopolysaccharides and with unusually high bacterial and cyanobacterial populations (Newton *et al*., 1994). In 1990, however, both flux events consisted of spring-bloom-type material. Boyd and Newton (1995) suggest that stronger flux rates during 1989 compared to 1990 were related to striking differences in the sizes of the dominant diatom species (large chain-forming diatoms including *Chaetoceras* in 1989; the 5 μm-sized diatom *Nanoneis* spp. during 1990). Finally, evidence is emerging for changes in flux intensity over longer time scales. At Station M (NE Pacific), decadal-scale trends in fluxes coincide with increased sea-surface temperatures (Smith and Kaufmann, 1999) while a decrease in opal flux relative to the carbonate flux over a 14-year time period (1978–1991) in the Sargasso Sea may be related to climatic trends (Deuser *et al*., 1995).

3.2 *Deposits on the seafloor*

During the late 1970s and early 1980s, patchy deposits of aggregated organic material ("phytodetritus") were photographed on the seafloor down to 5000 m water depth on the Porcupine Abyssal Plain and at other sites in the Rockall Trough and Porcupine Seabight using a camera attached to an epibenthic sledge and collected using the Barnett-Watson multiple corer (Barnett *et al*., 1982; Billett *et al*., 1983; Rice *et al*., 1986). These observations provided the first direct evidence that pulsed fluxes of material through the water column can accumulate as visible deposits on the seafloor (Gooday and Turley, 1990). The arrival of this material during late spring and early summer, and its subsequent disappearance during the course of the summer, were also documented using time-lapse photography (Lampitt, 1985). Later studies confirmed that seasonal phytodetritus deposition is widespread at temperate latitudes (north of ~34–41°N) in the NE Atlantic (e.g. Thiel *et al*., 1989; Rice *et al*., 1994; Auffret *et al*., 1994; Turley *et al*., 1995), NW Atlantic (Hecker, 1990), as well as further north in the Greenland-Norwegian Sea (Graf, 1989; Graf *et al*., 1995) and northern Barents Sea (Pfannkuche and Thiel, 1987). In the temperate abyssal NE Atlantic, these deposits deliver an estimated 2–4% of spring-bloom production to the seafloor (Turley *et al*., 1995). In the equatorial Pacific, 2–9% of the annual POC flux to the seafloor may be associated with nearly intact phytoplankton and 25–100% with general phytodetritus, although these estimates assume the phytodetritus deposition occurs throughout the year (Stephens *et al*., 1997).

The spring bloom is usually well-developed in the temperate and subarctic North Atlantic and gives rise to a strong phytodetrital signal at the seafloor (Campbell and Aarup, 1992; Longhurst *et al*., 1995; Lampitt and Antia, 1997; Longhurst, 1998). However, this process is not confined to the North Atlantic. Bentho-pelagic coupling appears to be particularly efficient at high latitudes in the Arctic (Ambrose and Renaud, 1995). A thick phytodetrital layer was observed in some bottom photographs from the Antarctic shelf and upper slope (Weddell Sea; 99–1243 m water depth), but coverage was very patchy in both time and space and was not related to the abundance of megafauna (Gutt *et al*., 1998). Phytodetrital layers were frequently observed on the tops of cores collected in the Arabian Sea during the German BIGSET programme (Pfannkuche *et al*., 2000). At Station M, located in the NE Pacific under the California Current, phytodetritus was most evident during summer and autumn when the flux of material into sediment traps moored 50 m and 600 m above the bottom was greatest (Smith *et al*., 1994). In a detailed time series study at this site extending over a number of years (1989–1996), various different kinds of deposit, including loosely and strongly cohesive aggregates, were recognised (Smith and Druffel, 1998). Between July 1990 and July 1991, the detrital aggregates occupied <1.5% of the seafloor in any one photograph, but collectively, they covered 25% of the seafloor over the course of this one year (Smith *et al*., 1994). In 1994, large detrital aggregates were present from July to September and white flocculent material carpeted the seafloor from July to November, the period of maximum flux recorded in the sediment trap moored 50 mab (Beaulieu and Smith, 1998; Lauerman and Kaufmann, 1998; Smith *et al.*, 1998). During this period, visually distinct aggregates covered up to 4.9% of the seafloor in any one photograph (Smith *et al.*, 1998). Increases in sediment community oxygen consumption (SCOC) at Station M predated the first appearance of obvious detritus in seafloor photographs, suggesting that POC is delivered in the form of small particles during the spring (April–June) (Smith *et al.*, 1994). There are also reports of phytodetritus deposition in an abyssal open ocean area of the equatorial Pacific (Gardener *et al.*, 1984; Smith, 1994; Smith *et al.*, 1996). Greenish deposit of finely-flocculent material and larger aggregates were visible in photographs and collected in multi-cores from a zone between 5°S and 5°N along the 140°W line. However, unlike the NE Atlantic and NE Pacific, the equatorial Pacific exhibits a relatively low degree of seasonality in primary production. Phytodetritus observed during November and December 1992 was probably deposited more or less continuously over a period of at least 100 days rather than as a distinct, time-limited pulse (Smith *et al.*, 1996). Possible sources are convergence zones, which result from equatorial upwelling and are intensified by the passage of tropical instability waves (Honjo *et al.*, 1995).

Phytodetrital aggregates generally contain fresh phytoplankton and cyanobacterial cells and pigments (Billett *et al.*, 1983; Thiel *et al.*, 1989; Smith *et al.*, 1996), indicating rapid delivery of material derived from surface blooms. The composition and physical characteristics of phytodetritus reflect the season of deposition, geographical location and seafloor processes. In the temperate North Atlantic, "typical" spring-early summer phytodetritus contains a high proportion of diatoms derived from the diatom-dominated spring bloom, in addition to a variety of other biogenic particles (Billett *et al.*, 1983; Thiel *et al.*, 1989). Phytodetritus deposited later in the year, however, is predominantly gelatinous and contains coccospheres and coccoliths and pigments characteristic of coccolithophorids, dinoflagellates and green algae (De Wilde *et al.*, 1998). At Station M (NE Pacific), aggregates were dominated by chain-forming diatoms in August 1994 but in September they contained numerous phaeodarian radiolarians, probably entrained during the passage of the aggregates through the water column (Beaulieu and Smith, 1998). Golf-ball-sized ("rad patch") aggregates most likely probably formed by the rolling of phaeodarian-rich detritus across the seafloor, allowing the radiolarian spines to entrap other particles (Beaulieu and Smith, 1998). This station is overlain by waters that form part of the California Current and have patterns of phytoplankton production that vary interannually. Sedimenting aggregates are also dominated by diatoms at high latitudes in the Northern and Southern hemispheres (von Bodungen *et al.*, 1986, 1995; Graf *et al.*, 1995). Like the settling fluxes recorded by sediment traps, phytodetritus deposits may vary substantially from year to year at a particular site. At Station M, flocculent material covered the seafloor from July to November 1994 but was less obvious in other years (Lauerman and Kaufmann, 1998). In the NE Atlantic, phytodetritus deposits have not been observed on the seafloor at the BENGAL site on the Porcupine Abyssal Plain since 1995, despite the maintenance of regular seasonal pulses of settling material caught in sediment traps during this period (Lampitt *et al.*, 2001).

3.3 Chloroplastic pigments in the sediments

Chlorophyll is one of the most labile components of particulate organic matter (Wakeham *et al.*, 1997; Stephens *et al.*, 1997). Concentrations of chlorophyll *a* and chloroplastic pigment equivalents (CPE; chlorophyll plus its degradation products) in sediment samples therefore provide good tracers for phytodetritus inputs to the seafloor (e.g. Thiel, 1983; Pfannkuche, 1985; Pfannkuche and Thiel, 1987; Smith *et al.*, 1996; Pfannkuche and Soltwedel, 1998; Pfannkuche *et al.*, 1999, 2000). Chlorophyll *a*, most of which has a degradation half life 4–120 days, can be used as a tracer for fresh phytoplankton-derived material at the seafloor (Stephens *et al.*, 1997).

Although CPE values integrate the flux signal over longer time periods (Pfannkuche *et al.*, 2000), they may still reflect seasonal patterns of sedimentation. In a record from the BIOTRANS area, pieced together from data collected during different years, CPE values were lowest in March 1985 and highest in June 1990 and July 1986 (Pfannkuche, 1993). On the shelf and upper slope on the Goban Spur off SW Ireland, Soltwedel (1997) and Pfannkuche and Soltwedel (1998) observed two peaks in CPE concentrations during the spring (May/June 1994) and late summer/autumn (August 1995, September 1994, October 1993). This pattern becomes barely detectable at 2200 m depth. Deeper sites on Pendragon Escarpment and PAP (3500–4500 m depth) show single CPE peaks in late summer. Seasonal and interannual variations in pigment concentrations were evident at the Porcupine Abyssal Plain during 1996–1998 (Witbaard *et al.*, 2000). High concentrations during September 1997 were associated with fresh phytodetritus (Witbaard *et al.*, 2000) but had dropped to much lower levels by March 1998. Phaeophorbide (but not chlorophyll *a*) values rose again in July 1997 but did not approach those measured in September 1996. In October 1997 and September 1998, concentrations of both pigments were similar to those from March 1998. At bathyal depths in Sagami Bay (Japan), CPE values in the upper cm of sediment peaked in the spring of 1997 and 1998; the thickness of the upper oxygenated sediment layer of sediment diminished correspondingly, although with a time lag of about a month (Shimanaga *et al.*, 2000).

Seasonal differences in chlorophyll *a* concentrations were less apparent in the deep Arabian Sea (Pfannkuche *et al.*, 2000). However, data from different years (March, October 1995, April 1997, February 1998) suggests that chlorophyll *a* values and chlorophyll *a*/pheopigment ratios (but not CPE values) are higher during the NE monsoon period (February–April) at the WAST site, presumably reflecting a pulse of relatively fresh phytodetritus.

3.4 Summary

Life on the ocean floor depends to a very large extent on bentho-pelagic coupling, i.e. the deposition on the seabed of organic-rich particles originating in the upper water column (reviewed by Gooday and Turley, 1990; Graf, 1992). Seasonal variations in particulate fluxes through the water-column are probably more or less ubiquitous, although the amplitude of the fluctuations, as well as the flux intensity, vary enormously in different oceanographic settings (Lampitt and Antia, 1997). The formation of visible deposits of settled material (“phytodetritus”) on the seabed usually (but not always) occurs in areas where primary production is highly seasonal. As a result, the appearance of these deposits is normally confined to periods following ocean-surface phytoplankton bloom. Water column fluxes and deposition events are often bimodal with one peak in spring/early summer and another one later in the year. Studies conducted over a number of years often reveal substantial interannual variations in the intensity of supply to the benthic community.

4. Consequences of Seasonal Organic Matter Inputs for Benthic Communities

4.1 Introduction

During its passage through the water column, phytodetritus undergoes biologically-mediated transformations, resulting in the loss of labile organic matter from the aggregates (Turley *et al.*, 1995; Wakeham *et al.*, 1997). Phytodetritus in the abyssal NE Atlantic yields surprisingly low total organic carbon (TOC) percentages (Rice *et al.*, 1986) but higher values (1–12.5% organic carbon = 5–39 times greater than underlying sediment) are reported from the equatorial Pacific (Smith *et al.*, 1996). These discrepancies may reflect differing amounts of time spent on the seafloor by the aggregates. Fresh phytodetritus, which contains phytoplankton and cyanobacterial cells and easily degradable chlorophyll pigments, is an important source of labile organic matter for benthic communities. There is a substantial and growing body of evidence suggesting that phytodetritus-mediated seasonal biological processes are widespread in the deep sea and profoundly influence benthic community structure and ecosystem functioning. Effects are seen at the community, higher taxon and species levels, within different faunal compartments, in physiological and reproductive processes, and in the behaviour of individual animals.

4.2 Benthic community and population responses

4.2.1 Sediment Community Oxygen Consumption (SCOC)

Rates of oxygen uptake reflect the overall response of benthic communities to fluxes within a small area of seafloor. SCOC is usually measured *in situ* using a free-vehicle grab respirometer (Smith *et al.*, 1979). Seasonal fluctuations in oxygen uptake values are expressed most clearly in the North Pacific Ocean. At an oligotrophic site in the central North Pacific (Station CNP; 5900 m water depth), and a eutrophic site in the eastern North Pacific (Station C; 3815 m depth), rates were significantly higher (4 and 2 times respectively) in summer than in winter months, these maxima coinciding with expected peaks in particle fluxes to the seafloor (Smith and Baldwin, 1984). Smith (1987) reports SCOC data obtained between November 1977 and February 1985 from these two stations and three additional North Pacific sites: Stations G (4900 m), F (4400 m) and SCB (1300 m). Together, these five stations form a transect from the California margin to the central North Pacific along which SCOC decreased from east to west (i.e. away from land). Although the data are patchy (measurements were rarely made during the same month at each station), SCOC values were significantly higher in June than earlier or later in the year (i.e. August to April), except at Station G where data are available for only three months. Studies extending over periods of several years at the intensively studied Station M off the Californian coast (4100 m water depth) have also revealed clear seasonal variations in SCOC values (Smith *et al.*, 1992, 1994). A pattern of SCOC minima early in the year and maxima in the summer/autumn, more or less coincident with the POC flux, has recurred consistently between June 1989 and October 1996 (Smith and Kaufmann, 1999). Overall, SCOC values varied by a factor of about 3 during this period, although the amplitude of variation was far from consistent between years.

Evidence for seasonally varying SCOC rates in other oceans is less compelling than for the Pacific. At the BIOTRANS site in the NE Atlantic, summer (July 1986, August 1989) SCOC rates were twice those measured during April 1988 (Pfannkuche, 1993), although the difference was not statistically significant. Graf (1989) detected a similar two-fold increase in oxygen consumption following a summer sedimentation event at 1430 m

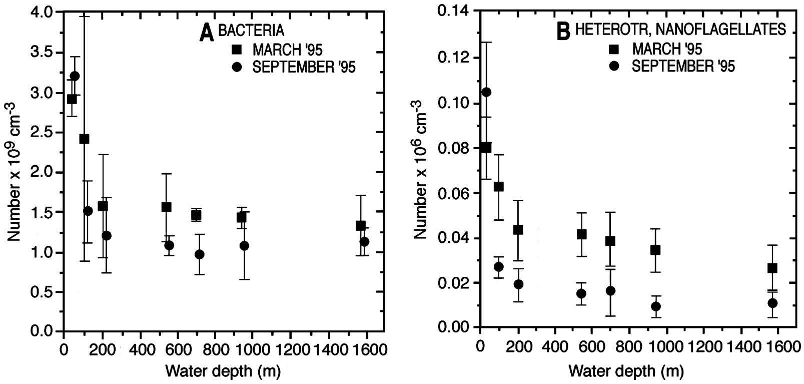

Fig. 3. Population densities of a) bacteria and b) heterotrophic flagellates along a downslope transect in the oligotrophic Cretan Sea (western Mediterranean). Bars indicate 95% confidence levels of means. Reprinted from *Progress in Oceanography*, **46**, G. C. A. Duineveld, A. Tselepides, R. Witbaard, R. P. M. Bak, E. M. Berghuis, G. Nieuwland, J. van der Weele and A. Kok, Benthopelagic coupling in the oligotrophic Cretan Sea, figures 3 and 4, p. 468, 469, © 2000 Elsevier Science Ltd, with permission from Elsevier Science.

on the Vøring Plateau (Norwegian margin). At an oligotrophic site near Bermuda (4400 m water depth), however, Sayles *et al.* (1994) were unable to detect significant seasonal variations in SCOC. Despite the presence of phytodetritus in some samples, a negative result was also obtained by Lampitt *et al.* (1995) who used a suspended core technique (Patching *et al.*, 1986) at a 2000 m station in the Porcupine Seabight (NE Atlantic). There was no detectable increase in SCOC on the Celtic continental slope following the 1994 spring bloom (Duineveld *et al.*, 1997). Witbaard *et al.* (2000) measured SCOC at the BENGAL station on the Porcupine Abyssal Plain using a benthic chamber attached to a lander. Values obtained during September 1996 (when fresh phytodetritus was present on the seafloor), March 1997, July 1997 and September 1998 were not statistically different. Further north in the Greenland-Norwegian Sea, oxygen profiles within the sediment indicate that organic carbon degradation rates are low and oxygen demand varies little over the seasonal cycle (Sauter *et al.*, 2001). Rather surprisingly, small (a factor of approximately two) temporal fluctuations in SCOC were observed at depths between 100 m and 1570 m in the Cretan Sea, despite the highly oligotrophic nature of this region (Duineveld *et al.*, 2000).

The lack of a response in some Atlantic studies may be because the seasonal signal was too ephemeral to be detected (Graf, 1992). It probably also reflects differences in the quality of the organic matter reaching the seafloor (Turley and Lochte, 1990; Sauter *et al.*, 2001). Modelling studies suggest that seasonal SCOC responses are sensitive to the overall reactivity of the organic matter. According to Martin and Bender's (1988) model, which is based on oxic mineralisation pathways, seasonal inputs of unreactive organic carbon result in SCOC fluctuations that are much smaller than variations in the carbon flux to seafloor. Using this model, Sayles *et al.* (1994) concluded that a SCOC response of the kind observed by Smith *et al.* (1992) at Station M on the Californian margin would require inputs of very labile material (rate constant 5–10 yr^{-1}). Soetaert *et al.* (1996) developed a more complex model in order to explore the effects of a seasonally fluctuating carbon flux on different pathways for the remineralisation of organic carbon and vertical profiles of oxygen and other electron acceptors in sediment. As organic carbon inputs increase, pulsed organic carbon inputs may initiate a series of reactions involving first oxygen, then nitrate, and finally anoxic processes, rather than being decomposed solely by oxic mineralisation. The relative contribution of these different oxidation pathways may change with time, leading to redox levels that fluctuate vertically within the sediment profile. These model studies (Martin and Bender, 1988; Soetaert *et al.*, 1996) suggest that labile organic matter fluxes lead to a more immediate and stronger geochemical and biological response than pulses of less reactive material. Gehlen *et al.* (1997) described striking changes in pore-water O_2, NO_3^- and Mn^{2+} profiles at the 2300 m-deep DYFAMED-BENTHOS site in the NW Mediterranean following an input of organic-rich sediments derived from the upper slope. Despite its dramatic geochemical effect, this input represented only 1% of the average organic carbon content of the surficial sediments.

4.2.2 Small organism responses

Benthic organisms are generally divided by size into the bacteria, nano-, meio-, macro- and mega-fauna. Following Soltwedel (1997) and Pfannkuche and Soltwedel (1998), it is convenient to consider "small organisms" (bacteria, fungi, flagellates, metazoan and protozoan meiofauna) under one heading. Fresh phytodetrital aggregates are a focus for intensified activity by bacteria and small flagellates (Lochte and Turley, 1988; Turley *et al*., 1988; Turley and Lochte, 1990; Smith *et al*., 1996). It is often bacteria that show the strongest and most rapid population response to seasonal organic matter inputs. Lochte (1992) reported a doubling of bacterial biomass between spring and summer samples from the BIOTRANS area. During the CINCS project, bacterial abundance and biomass (0–1cm layer) showed a distinct response to seasonal changes in the quality and quantity of sedimented organic particles in the bathyal Cretan Sea (500–1540 m water depth), with highest values being observed in February 1995 (Danavaro *et al*., 1999, 2000b). Duineveld *et al*. (2000) report increases in bacterial abundance during March compared with September 1995 at all except the shallowest station along the same transect (i.e. 100–1570 m depth) (Fig. 3). Heterotrophic flagellates, which probably prey on the bacteria, showed a similar pattern. *In situ* tracer experiments using ^{13}C labelled diatoms (Levin *et al*., 1999), ship-board feeding experiments (Altenbach, 1992), and measurements of biochemical parameters such as ATP (Linke, 1992; Linke *et al*., 1995) indicate that deep-sea benthic foraminifera are also highly responsive to food pulses (Gooday *et al*., 1992). Some species, particularly those with calcareous shells, undergo short-term changes in population density that are related to seasonal inputs of labile organic matter (reviewed by Gooday and Rathburn, 1999; see also Newton and Rowe, 1995; Kurbjeweit *et al*., 2000; Kitazato *et al*., 2000). Most examples are from bathyal settings on continental margins, although abyssal, open-ocean species exhibit similar population fluctuations in areas of seasonal phytodetritus deposition (Gooday and Turley, 1990; Gooday and Rathburn, 1999; Kurbjeweit *et al*., 2000). The species concerned are usually small, thin walled epifaunal or shallow infaunal calcareous form, which probably have opportunistic life-history characteristics (Gooday, 1993).

In addition to time-consuming direct observations, various biochemical parameters provide a comparatively rapid way to measure the activity and biomass of small organisms. Useful parameters include esterase turnover rates with flourescein-di-acetate (FDA) for bacterial enzymatic activity, total adenylates (ATP + ADP + AMP), DNA, phospholipids and proteins for biomass of small organisms (Pfannkuche, 1993; Soltwedel and Thiel, 1995; Soltwedel, 1997). These methods reveal that small benthic organisms (probably mainly protozoans and bacteria) can respond in terms of biomass and activity within days of the arrival of organic matter pulses (e.g. Graf, 1989; Soltwedel, 1997). The first detectable benthic response is often the initiation of bacterial extracellular enzyme activity (Boetius and Lochte, 1994; Poremba and Hoppe, 1995). In the deep sea, this precedes the production of any bacterial biomass by at least several days (Boetius and Lochte, 1996).

Population level responses to food pulses by the metazoan meiofauna have proved more elusive than those of bacteria and protozoans (Soltwedel, 2000), perhaps because metazoans have a slower turnover rate. Pfannkuche (1992, 1993) was unable to detect any seasonal changes in total metazoan meiofaunal densities or biomass in the BIOTRANS area. There are indications, however, that pulsed inputs may trigger growth and reproduction at this site. Soltwedel *et al*. (1996) report seasonal changes (compiled from several year's data) in nematode size spectra. Body length and volumes increased from April 1984 to a peak in July 1986 and then decreased in August 1989 and further in September 1985. Nematode sizes also exhibited greater variation between replicates in August 1989 (BIOTRANS site) than in May 1988 (Porcupine Abyssal Plain site), possibly reflecting reproductive activity during the summer triggered by phytodetritus inputs. Soltwedel *et al.* (1996) speculate that nematodes at these abyssal sites grow in body size during spring and early summer. They suggest that reproduction during the late summer is followed by the death of the adults, leading to the populations dominated by the small, individuals observed in September. At a bathyal site in the Porcupine Seabight, the abundance of most meiofaunal taxa was similar in samples collected in April and July 1983, before and after the spring bloom (Gooday *et al*., 1996). Vertical distribution patterns within the sediment were virtually identical in the two sets of samples. The significantly greater numbers of nauplii in the July samples, however, suggested a possible reproductive response by harpacticoid copepods. Sommer and Pfannkuche (2000) found no relation between nematode abundance and POC-chlorophyll *a* flux in the Arabian Sea, although there were correlations with biomass, individual size and vertical distributions within the sediment. In the Cretan Sea (eastern Mediterranean), Danovaro *et al*. (1999, 2000c) reported a clear and rapid increase in the metazoan meiofaunal abundance and biomass on the shelf (40–100 m depth) following the maximum organic matter flux in February. The response at deeper-water sites (540–1540 m depth), however, was much less obvious. Between February and May 1995, there was a slight and non-significant increase in densities of total meiofauna and some higher taxa. Increases also occurred in the density of nauplii (May) and harpacticoids (September), suggesting a time-lagged reproductive response to the February food input. The lack of a strong metazoan response at the deeper sites suggests that bacteria dominate benthic processes in this highly oligotrophic system. At a much more eutrophic bathyal site (1450 m depth) in Sagami Bay (Japan), copepods and kinorhynchs (but not polychaetes and nematodes) were located closer to the sediment surface when CPE values (reflecting seasonal food inputs) were higher, suggesting that they migrate up through the sediment in search of food (Shimanaga *et al.*, 2000).

The best evidence for a population level response by deep-sea metazoan meiofauna comes from the ECOMARGE (Gulf of Lions) and DYFAMED-BENTHOS (Ligurian Sea) projects in the NW Mediterranean. In the Gulf of Lion on the Catalan margin, total metazoan meiofaunal numbers increased twofold between late summer (end of August) and early winter (late November/early December) in cores from canyons on the upper slope and deeper parts of the continental margin (672–2300 m water depth) (de Bovée *et al.*, 1990). During this period, there was a corresponding increase in chloroplastic pigment concentrations, particularly in the canyons where organic matter deposition rates were enhanced. At the 2300 m-deep Ligurian Sea site, Guidi-Guilvard *et al.* (2000) report that 54% of variance in metazoan meiofaunal abundance was due to temporal variability. Population changes were related to seasonally varying particle fluxes. Densities increased over a period of a month following peak inputs.

4.2.3 Larger organism responses

Because of their larger size and generally longer life histories, obvious macro- and mega-faunal population responses to pulsed food inputs are more difficult to establish. Separating spatial and temporal abundance patterns is also problematic for larger animals (Pfannkuche, 1993), particularly the megafauna (Lauerman and Kaufmann, 1998). Pfannkuche (1992, 1993) was unable to detect seasonal variations among the macrofauna at the BIOTRANS site because spatial variation within samples collected during one cruise was higher than temporal differences. Significantly higher macrofaunal densities were reported by Flach and Heip (1996) in samples from May 1994 compared to those from August 1995 and October 1993 at depths down to ~1500 m on the Goban Spur, SW of Ireland. This difference, however, was due mainly to large numbers of juveniles of the ophiuroid *Ophiocten gracilis*, a seasonally reproducing species (Sumida *et al.*, 2000). Polychaete densities were significantly higher in May than in August at ~210 m and ~670 m, and somewhat higher in May at ~1500 m. Since the samples were taken in different years, however, these differences may reflect interannual rather than seasonal differences. Drazen *et al.* (1998) reported the first good evidence for seasonal changes in macrofaunal densities. At Station M, macrofaunal foraminiferal densities increased moderately between October 1989 and February 1990 and rose substantially between October 1990 and February 1991 in samples collected using a free vehicle grab respirometer. Although seasonal changes in total metazoan macrofaunal densities were not significant, five taxa (nematodes, polychaetes, harpacticoid, tanaids, isopods) retained on a 300 μm screen exhibited significant density increases between June and February in one or both years. Peak macrofaunal densities occurred following the disappearance of detrital aggregates from the seafloor and about 8 months after maximal SCOC and flux values.

Seasonality has also been reported for the epibenthic/benthopelagic megafauna in the Benthic Boundary Layer (BBL) on the continental slope in the western Mediterranean off the Catalan coast. This area is characterised by submarine canyons in which biomass tends to concentrate. Cartes *et al.* (1994) described seasonal changes in the abundance and composition of the megafauna, and mesopelagic crustaceans, caught in bottom trawls at upper slope (245–485 m water depth), middle slope (514–730 m) and canyon (430–415 m) sites. Megafaunal biomass within the canyons was higher during the spring, possibly as a result of fluctuations in the food supply. Seasonal changes in the biomass of fish and crustacean megafauna were reported by Sardà *et al.* (1994) in upper slope canyons (410 m) and at middle (600–650 m) and lower slope (1200 m) locations in the same area. At the deepest site (1200 m), however, seasonal changes were less evident and only fish biomass fluctuated significantly. Cartes (1998) found that decapod abundance and biomass were higher during the spring, and fish biomass was higher in the autumn, on the Catalan margin. Again, these changes were most evident on the upper (390–508 m depth) and middle (545–692 m depth) slope. They were linked to seasonal fluctuations in the densities of benthopelagic macrofauna (mainly crustaceans) that live within the benthic boundary layer and are prey for the megafauna. The BBL macrofauna at two sites (~2400 m, 3000 m water depth) in the Cap-Ferret Canyon (SE Bay of Biscay) also exhibited clear seasonal maxima in epibenthic sledge samples taken in May 1991 compared to those from July 1989 and August 1991 (Sorbe, 1999). These differences were attributed to a benthic response to peak organic fluxes during the spring.

4.3 Foraminiferal assemblage response

In addition to the species response mentioned above, the composition of foraminiferal faunas also reflects the pulsed nature of organic matter fluxes in areas with strong seasonal cycles in primary production. Loubere (1998) compared assemblages from locations in the Pacific and Indian Oceans (water depths 2100–3500 m) where the environmental conditions were similar except in one respect; seasonality was low at the Pacific sites and high at the Indian Ocean sites. In areas of high productivity, he found that certain taxa (*Uvigerina* spp., *Chilostomella* sp., *Pullenia* sp., *Eponides tumidulus*) were less common whereas others (*Epistominella exigua*, *Cassidulina hooperi*, *Gyroidina* spp., *Bulimina mexicana* and *Nonion* spp.) were more common in the Indian than in the Pacific Ocean. He attributed these differences to increasing seasonality in organic matter fluxes at higher productivity levels. Loubere and Fariduddin (1999a, b) analysed a global foraminiferal dataset from the Atlantic, Pacific and Indian Oceans (depth range 2300–3600 m). Assemblage composition was positively correlated with seasonality (defined by an index based on ocean-surface pigment concentrations). Using discriminate function analysis they were able to recognise assemblages associated with (i) low seasonality combined with higher flux levels, (ii) strong seasonality with a single productivity pulse, and (iii) strong seasonality with multiple productivity pulses. Hispid forms of *Uvigerina* were more abundant under low seasonality regimes, *C. hooperi*, *Gyroidina* spp., *B. mexicana* and *Nonion* spp. under seasonal regimes with a single productivity pulse, while *E. exigua* and *Alabaminella weddellensis* were associated with multiple productivity pulses. The excellent fossil record of benthic foraminifera, and the existence of good databases on their relation to organic matter fluxes and seasonality (Altenbach *et al*., 1999; Loubere and Fariduddin, 1999b), means that these protozoans can be used to recognise seasonality on palaeoceanographic record (e.g. Smart *et al*., 1994; Thomas and Gooday, 1996).

4.4 *Reproductive responses*

Where evidence is available, most deep-sea invertebrates appear to breed asynchronously (e.g. Rokop, 1974, 1977b; Tyler *et al*., 1985; Tyler, 1986; Gage and Tyler, 1991; Tyler and Young, 1992; Blake and Watling, 1994; Scheltema, 1994; Ambrose and Renaud, 1997), in contrast to shallow-water temperate marine systems where seasonal reproduction is normal. Asynchronously breeding echinoderms produce large (>600 μm) eggs which develop directly into juveniles without a larval stage (Tyler, 1986). However, certain species belonging to a number of higher taxa (Spongia, Actiniaria, Polychaeta, Isopoda, Decapoda, Cumacea, Brachiopoda, Bivalvia, Scaphopoda, Asteroidea, Ophiuroidea, Echinoidea, fish) exhibit seasonally synchronous reproductive cycles, seasonal peaks in reproductive intensity, or seasonal recruitment (reviewed in Tyler, 1986, 1988, 1996; Harrison, 1988; Gooday and Turley, 1990; Gage and Tyler, 1991; Tyler *et al*., 1992a; Eckelbarger and Watling, 1995; summarised in Table 2 herein). Most examples of seasonal reproduction in deep-sea animals are from continental margin settings, usually at depths shallower than 3000 m, rather than from abyssal, open-ocean areas. Indeed, some of the species have bathymetric ranges which extend onto the shelf and can hardly be considered as true deep-sea taxa (Gage *et al*., 1986; Harrison, 1988).

Reproductive seasonality in deep-sea invertebrates, particularly echinoderms, has been studied intensively by P. A. Tyler, J. D. Gage and colleagues on the basis of an extensive programme of time-series sampling from bathyal depths in the Rockall Trough (UK continental margin). Among the echinoderms examined, there is good evidence for seasonal patterns in two ophiuroids (*Ophiura ljungmani*, *Ophiocten gracilis*), an asteroid (*Plutonaster bifrons*) and three echinoids (*Echinus affinis*, *E. acutus* var. *norvegicus* and *E. elegans*) (Gage and Tyler, 1981a, 1991; Tyler and Pain, 1982; Tyler and Gage, 1982, 1984; Tyler *et al*., 1982, 1990; Gage *et al*., 1986; Tyler, 1986, 1988; Sumida *et al*., 2000) (Table 2). The asteroid *Dytaster grandis* from the abyssal (4000 m) NE Atlantic also reproduces seasonally (Tyler *et al*., 1990) and *D. insignis*, its bathyal counterpart in the Rockall Trough, may have a similar cycle (Tyler and Pain, 1982). Unlike continuously-breeding echinoderms, these species produce small eggs (100–120 μm) and have planktotrophic larvae. There is also good evidence for seasonal patterns of recruitment and gametogensis in the anenome *Amphianthus inornata* (Bronsdon *et al*., 1993), two protobranch bivalves *Yoldiella jeffreysi* and *Ledella pustulosa* (formerly *L. messanensis*) (Lightfoot *et al*., 1979; Tyler *et al*., 1992b) and the spider crab *Dorhynchus thomsoni* (Hartnoll and Rice, 1985; Hartnoll *et al*., 1987) from the Rockall Trough; the evidence is more tenuous in the case of asellote isopods (Harrison, 1988). In the nearby Porcupine Seabight, the crab *Geryon trispinosus* exhibits seasonal patterns in egg laying, hatching and larval settlement (Attrill *et al*., 1991). Seasonal patterns in reproduction and reproductive behaviour (pairing) appear to be relatively common among upper bathyal (400–900 m water depth) echinoderms (particularly echinoids) in the western Atlantic off the Bahamas (Young *et al*., 1992; Tyler and Young, 1992). Seasonal reproduction in other deep-sea invertebrate species has been reported in the Arctic, western Mediterranean, NW Atlantic and NE Pacific (Table 2).

Seasonal reproduction in NE Atlantic invertebrates may be linked to spring/early inputs of phytodetritus and other food sources in a region where the spring bloom is very well developed (Tyler and Gage, 1980; Tyler *et al*., 1982). One such species, the echinoid *Echinus affinis* forages for fresh phytodetritus during the summer (Billett *et al*., 1983; Campos-Creasey *et al*., 1994). Analyses of stomach contents suggest that the bivalve *Ledella pustulosa* also feed on phytodetritus (Tyler *et al*., 1992b) while the asteroid *Plutonaster bifrons* consumes the seasonally-delivered remains of blue whiting (Tyler *et al*., 1993). Pulsed food inputs could trigger a number of reproductive process: 1) the initiation of gametogenesis; 2) the development of gametes including the accumulation of yolk (vitellogenesis); 3) spawning; 4) larval settlement (Tyler *et al*., 1982). In *Dytaster grandis* (an abyssal asteroid) and *Plutonaster bifrons* (a bathyal as-

Table 2. Examples of seasonal reproductive and recruitment in deep-sea invertebrates.

Higher taxon	Species	Locality	Evidence for seasonal reproduction or recruitment	Reference
Pisces	*Nezumia aequalis*	NE Atlantic, Rockall Trough; 700–1250 m	Spawning April–October	Gordon (1979)
Pisces	*Trachyrhynchus murrayi*	Rockall Trough, 1000–1500 m	Spawning March–April	Gordon (1979)
Pisces	*Lepidion eques*	Rockall Trough, 500–1250 m	Spawning April–May	Gordon (1979)
Pisces	*Coryphaenoides rupestris*	Rockall Trough and Hatton Bank	Spawning April–May	Geistdoerfer (1979)
Asteroidea	*Dytaster grandis*	Rockall Trough, 2900–4400 m	Oogenesis initiated Feb.–early April; synchronous spawning early in year; vitellogenesis and settlement of planktotrophic larvae linked to phytodetritus	Tyler *et al.* (1990)
Asteroidea	*Plutonaster bifrons*	Rockall Trough, 2200 m	Gametogenesis initiated spring; maximum vitellogenesis summer/autumn; spawning March–June. Many small eggs; settlement of presumed planktotrophic larvae linked to phytodetrital fluxes	Tyler & Pain (1982); Tyler *et al.* (1993)
Ophiuroidea	*Ophiura ljungmani*	Rockall Trough, 2,900 m	Gametogenesis initiated Feb./March; rapid vitellogenesis Oct.–Jan.; synchronous spawning late Jan.–Feb.	Tyler & Gage (1980)
Ophiuroidea	*Ophiomusium lymani*	Rockall Trough, 2200 m	No periodicity in egg formation but annual periodicity in recruitment linked to phytodetritus sedimentation	Gage & Tyler (1982)
Ophiuroidea	*Ophiocten gracilis*	Rockall Trough, 700–2000 m; Faeroe Islands, 170–780 m	Gonad development highly seasonal; spawning late winter early spring; larvae in spring plankton samples; juveniles recruited late spring/summer	Gage & Tyler (1981a); Tyler & Gage (1982); Sumida *et al.* (2000)
Echinoidea	*Brissopsis lyrifera*	NW Mediterranean, Gulf of Lions, 60–930 m	Gametogenesis begins in spring; males & females mature by end of summer, spawning at beginning of autumn, winter period of gonadal inactivity	Féral *et al.* (1990)
Echinoidea	*Echinus affinis*	Rockall Trough, 2200 m	Gametogenesis initiated Nov.–Dec. and continues for 12–14 months; vitellogensis in summer/autumn; spawning Jan.–Feb.; many eggs small, recruitment of presumed planktotrophic larvae in May	Tyler & Gage (1984); Campos-Creasey *et al.* (1994)

Table 2. (continued).

Higher taxon	Species	Locality	Evidence for seasonal reproduction or recruitment	Reference
Echinoidea	*Echinus acutus var. norvegicus*; *E. elegans*	Rockall Trough, 220–1075 m	Similar to *E. affinis*	Gage *et al.* (1986)
Echinoidea	*Stylocidaris lineata*	NW Atlantic, off Bahamas, 510–640 m	Breeding aggregations observed in May 1988, May–June 1989, Feb. 1990 but never in autumn; spawning occurs in spring	Young *et al.* (1992)
Decapoda: Bachyura	*Geryon trispinosus*	NE Atlantic, Porcupine Seabight, 490–1883 m	Egg laying Sept.–Oct; females incubate eggs over winter; hatching in May; settlement August–Sept.	Attrill *et al.* (1991)
Decapoda: Brachyura	*Dorhynchus thomsoni*	Porcupine Seabight, 1200 m	Ovarian development (vitellogenesis) April–July; eggs laid on pleopods summer-autumn; eggs hatch March–June following year; larvae and 1st crab instar occur pelagically July–September	Hartnoll & Rice (1985); Hartnoll *et al.* (1987)
Decapoda: Anomura	*Parapagurus pilosimanus*; *Catapaguroides microps*	Off west coast of Florida	"Reproduction seasonal"	Ahlfeld in Tyler (1988)
Isopoda	Species not differentiated	Rockall Trough, 1000–2900 m; mainly ~2900 m	Breeding activity occurs throughout year but intensity is seasonal; brooding females 25% in winter vs 7% in summer; vitellogenesis coincides with deposition of phytodetritus	Harrison (1988)
Isopoda	*Eurycope brevirostris*	Arctic Ocean, 768–1588 m	Brooding females most common in June; frequency of manca (early juvenile) stages decreases from June to Nov.	Brandt *et al.* (1994)
Isopoda	*Munnopsurus atlanticus*	W. Med., Catalan Sea, 383–1022m; Bay Biscay (Cap-Ferret Canyon) 354 m, 739 m	Breeding activity continuous but intensity seasonal; max. densities of brooding females in July (Biscay), maximum recruitment of manca stage in April (Biscay), April and December (Catalan Sea), possibly coinciding with maximum abundance of food (foraminifera) following phytodetrital flux	Cartes *et al.* (2000); Elizalde *et al.* (1999)
Cumacea	*Leucon profundus*	Rockall Trough, 2900 m	Early vitellogenesis April–June; later vitellogenesis July–September; mating early in year; release of juveniles late spring/early summer	Bishop & Shalla (1994)
Cumacea	*Leucon longirostris*	W. Mediterranean, Catalan Sea, 550–600 m	Breeding females and adult males most abundant in summer; recruitment late winter/early spring, possibly synchronized with phytodetritus deposition	Cartes & Sorbe (1996)

Higher taxon	Species	Locality	Evidence for seasonal reproduction or recruitment	Reference
Bivalvia	*Ledella pustulosa*	Rockall Trough, 2900 m	Gonads develop during summer/autumn, become fully mature by Jan.; spawning in winter; larvae probably lecithotrophic	Lightfoot *et al.* (1979); Tyler (1988); Tyler *et al.* (1992b)
Bivalvia	*Yoldiella jeffreysi*	Rockall Trough, 2900 m	Gonads become mature in October; spawning in winter; larvae probably lecithotrophic	Lightfoot *et al.* (1979); Tyler *et al.* (1992b)
Scaphopoda	*Cadulus californicus*	NE Pacific; San Diego Trough; 1100–1260 m	Oogenesis initiated late summer (1970) to early autumn (1971); spawning between July and October (1971)	Rokop (1974, 1977a)
Polychaeta	*Aurospio dibranchiata*	NW Atlantic, N. Carolina (2000 m) and Massachusetts (1250–2100 m) slopes	Seasonal egg production (eggs largest in November) but recruitment apparently occurs throughout year	Blake & Watling, (1994)
Brachiopoda	*Frieleia halli*	NE Pacific; San Diego Trough; 1060–1240 m	Oogenesis initiated early Autumn 1970–1972; spawning January–April of following year; cycle consistent over 3 yrs; larval settlement occurs throughout year	Rokop (1974, 1977a)
Actiniaria	*Paracalliactis stephensoni*	Bay of Biscay, 2000 m	Spring spawning indicated by (i) sperm development maximum April/May; (ii) % mature oocyctes decreases sharply from April to May	Van-Praet (1985, 1990)
Actiniaria	*Phelliactis hertwigi* *P. robusta*	Porcupine Seabight, 700–2200 m	Vitellogenesis Feb.–July, spawning Oct./Nov. (*P. hertwigi*); vitellogenesis in summer, spawning April/May (*P. robusta*)	Van-Praet *et al.* (1990)
Actiniaria	*Amphianthus inornata*	Rockall Trough, 2200 m	Oocyte size increases from May/June to Jan./Feb., suggesting that spawning occurs in Feb.–April	Bronsdon *et al.* (1993)
Spongia	*Thenea abyssorum*	Greenland-Norwegian Sea, ~2300 m	Onset of yolk development coincident with maximum particle flux	Witte (1996)

teroid), vitellogenesis may be supported by the consumption of seasonal food pulses during the summer (Tyler *et al.*, 1990, 1993). Tyler and Pain (1982), Tyler and Gage (1980), Tyler *et al.* (1990) further suggested that the timing of spawning (January–early March) in *D. grandis*, *P. bifrons*, and the ophiuroid *Ophiura ljungmani* allows planktotrophic larvae time to develop to take advantage of the peak phytodetrital flux in the lower water column. Summer recruitment of planktotrophic larvae occurs among a number of other seasonally reproducing species in Rockall Trough (Harrison, 1988). Links have been proposed between phytodetritus deposition and spawning in the anenome *Paracalliactis stephensoni* (Van-Praet, 1990) and the onset of yolk accumulation in the sponge *Thena abyssorum* (Witte, 1996). The synchronous recruitment of larval individuals of a small opheliid polychaete species following phytodetrital inputs in 1991 and 1996 at the Porcupine Abyssal Plain (BENGAL site) may result from an opportunistic reproductive response to food pulses (Vanreusel *et al.*, 2001). At Station M in the NE Pacific, the proportion of small individuals of the holothurian *Peniagone* sp. visible in photographs increased substantially from October 1994 to June 1995 following a major phytodetrital pulse during the summer and autumn of 1994, suggesting a possible reproductive response (Lauerman and Kaufmann, 1998). Many echinoids living at bathyal depths around the Bahamas exhibit seasonal reproduction (Tyler, 1996) and seasonal pairing behaviour has been reported in one of these species, *Stylocidaris lineata* (Young *et al.*, 1992). The deposition of macrophyte material in this region, which seems to be associated with the hurricane season (Wolff, 1979; Young in Tyler, 1996), provides a possible cue (Tyler and Young, 1992).

There is, nevertheless, "no evidence directly linking seasonal organic input and the immediate reproductive response of deep-sea macro- and mega-fauna" (Eckelbarger and Watling, 1995). This led Eckelbarger and Watling to emphasise the primary role of phylogeny in determining temporal patterns of invertebrate reproduction. They argue that the phylogenetic history of a species determines a number of its key biological and physiological attributes, such as the ability to process nutritionally rich food, to store organic nutrients and release them to the gonads, the pace of vitellogenesis and hence the rate at which oogensis (egg production) can be completed. Together, these genetically-embedded characteristics control the rate of conversion of food into eggs. Fast egg producers will exhibit a rapid reproductive response to food pulses but slow egg producers, which include most deep-sea echinoderms, will not. In the latter case, organic inputs may influence the overall level of fecundity but not the timing of reproduction. Within the framework imposed by these phylogenetic constraints, Eckelbarger and Watling (1995) and others authors (e.g. Gage and Tyler, 1991; Tyler and Young, 1992; Tyler *et al.*, 1994; Bishop and Shalla, 1994) recognise several possible reproductive responses to pulsed food inputs (Fig. 4).

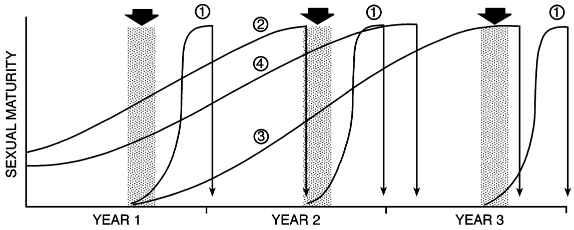

Fig. 4. Four types of reproductive pattern that might occur in deep-sea metazoan species in relation to seasonal pulses of phytodetritus to the seafloor (indicated by broad arrows and shaded bands). 1) Fast egg-producing species that respond immediately with rapid oogenesis and spawning. 2) Slow egg-producing species that spawns during seasonal pulse. 3) Slow egg-producing species that initiates gametogenesis in response to seasonal pulse. 4) Slow egg-producing species that shows no coordination of gametogenesis or spawning with seasonal pulse. Reprinted from *Invertebrate Biology*, **114**, K. L. Eckelbarger and L. Watling, Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates, figure 3, p. 265, © 1995 American Microscopical Society, with permission from the American Microscopical Society and the authors.

1) Gametogenesis may be initiated immediately after phytodetrital inputs with spawning occurring soon afterwards. Although there are no examples of this pattern among megafauna (Eckelbarger and Watling, 1995), except perhaps sponges (Witte, 1996), it may occur in some macrofaunal species, e.g. opportunistic polychaetes which are abundant in natural and artificial organically enriched patches in the deep sea (Grassle and Morse-Porteous, 1987; Snelgrove *et al.*, 1992, 1994, 1996). The cumacean *Diastylis stygia* exhibited a strong pulse of recruitment on the Atlantic slope off North America during April 1985 (Blake and Watling, 1994). Opportunistic life-history patterns are also found among foraminifera (meiofaunal protozoans) in which the reproductive process is simpler in the sense of not involving egg formation (Gooday and Turley, 1990; Gooday *et al.*, 1996).

2) Larval feeding and ontogeny may be timed to coincide with seasonal inputs because these provide conditions suitable for the development and survival of planktotrophic larvae. This pattern may apply to echinoderm species with this kind of larval development (Tyler *et al.*, 1982).

3) Seasonal inputs may initiate synchronised vitellogenesis, leading to an extended but fixed period of gametogenesis terminated by an eventual spawning event.

Tyler (1988) suggests this as a possible explanation for seasonal reproduction in deep-sea echinoderms and other invertebrates that produce eggs at a slow rate.

4) In the final pattern, which probably applies to many deep-sea macro- and mega-faunal species, reproduction is not related to pulsed food inputs. Presumably, these species either feed below the sediment surface and therefore do not consume fresh phytodetritus, or they lack the ability to convert its labile components into egg production.

Seasonal reproductive processes and seasonal recruitment do not necessarily go together. In populations of the polychaete *Aurospio dibranchiata* on the NE American margin, the largest eggs were found in November, suggesting seasonal egg production. Recruitment, however, apparently occurred throughout the year since small size classes were present during all three sampling periods (April, November and July) (Blake and Watling, 1994). The echinoid *Echinus affinis* reproduces seasonally but recruitment varies from year to year and there is high post-larval mortality (Tyler, 1988). Conversely, recruitment may be seasonally pulsed even when reproduction is not seasonal. Gage and Tyler (1982) studied of growth and reproduction in the ophiuroid *Ophiomusium lymani* from the Rockall Trough. The lack of seasonal periodicity in oocyte size frequency distributions suggests that this species produces gametes throughout the year. Samples taken during the summer, however, were dominated by newly metamorphosed larvae, indicating enhanced recruitment during this period. Gage and Tyler resolved this contradiction by suggesting that larval settlement is enhanced in response to seasonal fluctuations in the sedimentation of organic matter to the seafloor.

4.5 *Growth-rate responses*

Evidence for seasonal variations in deep-sea growth rates is relatively sparse. The availability of labile organic matter appears to lead to an increase in the growth rate of the Rockall Trough ophiuroid, *Ophiura ljungmani*. This species, which unlike *Ophiomusium lymani* reproduces seasonally, grows fastest during the spring (Tyler and Gage, 1980; Gage and Tyler, 1981b). Growth lines or zones developed on carbonate structures can yield clues about growth patterns (Tyler, 1988). Growth zones on skeletal plates of the regular echinoids *Echinus affinis*, *E. acutus* var. *norvegicus* and *E. elegans* and the irregular echinoids *Echinosigra phiale* and *Hemiaster expergitus* from the Rockall Trough probably reflect seasonally enhanced growth rates during the spring and early summer when phytodetritus is present on the seafloor (Gage and Tyler, 1985; Gage *et al*., 1986; Gage, 1987). The three *Echinus* species reproduce seasonally, but there is no evidence for seasonal reproduction in the two irregular echinoids. Similar zones have been observed in arm ossicles of the Rockall Trough ophiuroids *Ophiura ljungmani* and *Ophiomusium lymani* (Gage, 1990) and skeletal plates of the crinoid *Bathycrinus carpenteri* from the bathyal Norwegian Sea (Duco and Roux, 1981). Growth lines ("growth checks") on shells of the brachiopod *Pelagodiscus atlanticus* from the Gay Head Bermuda transect (NW Atlantic; 2500–5000 m depth) (Zezina, 1975), the protobranch bivalves *Yoldia thraciaformis*, *Nuculana pernula* from the Carson Canyon (NW Atlantic; 900–1500 m depth) (Hutchings and Haedrich, 1984), *Ledella messanensis* and *Yoldiella dissimilis* from the Rockall Trough (Gage, 1985), and the fish *Nezumia aequalis* (Rannou, 1976), may also reflect seasonally fluctuating growth rates.

Direct evidence that phytodetritus fuels increased growth rates comes from time-lapse camera (BATHYSNAP) observations of the barnacle *Poecilasma kaempferi* (Lampitt, 1990), a rapidly growing deep-sea species (Green *et al*., 1994) for which there is some evidence for seasonal reproduction in the Rockall Trough (Williams and Moyse, 1988). An individual of this species grew in length from less than ~1 mm to 10 mm in six months at 1,526 m depth on the Goban Spur in the NE Atlantic. The rate of growth increased sharply after the middle of May when phytodetritus first appeared on the seafloor.

4.6 *Behavioural responses*

Seasonal changes in behaviour are reported for deep-sea fish. By using ingestable acoustic transponders and the AUDOS fish-tracking system, Priede *et al*. (1994) discovered that *Coryphaenoides armatus* took longer to arrive at bait, stayed longer, and swam more slowly in the early spring (February 1990, 1992), prior to inputs of phytodetritus in the eastern North Pacific (Station M), than later in the year (October 1991). These observations were not replicated in the NE Atlantic where arrival times at baits and swimming speeds of *C. armatus* and *Histiobranchus bathybius* were similar in the spring (April) and summer (August) (Smith *et al*., 1997). These seasonal comparisons of swimming speeds were based on values from different years. Data obtained within the same year and over a series of years are required in order to understand seasonal changes in the activity levels of scavenging fish (Priede and Bagley, 2000).

Aggregation of the echinoid *Echinus affinis* around phytodetrital patches have been observed in the NE Atlantic (Campos-Creasey *et al*., 1994) but aggregations of echinoderms were not evident at Station M (NE Pacific) where deposits of flocculent phytodetritus were more persistent and evenly distributed (Lauerman and Kaufmann, 1998). However, the ophiuroid *Ophiura bathybia*, which is usually partly buried, did emerge above the sediment surface when phytodetritus was abundant at this site (Lauerman and Kaufmann, 1998). Smith *et al*. (1994) report varying rates of activity (movement) in mobile megafauna (mainly holothurians) photographed over a 386 day period at Station M. The animals were more active in the summer when detrital coverage of the seafloor was at its highest and were occasionally observed directly associated with aggregates. Two small holothurian species (*Peniagone vitrea* and *Elpidia minutissima*) spent less time within the field of view of time-lapse cameras during the autumn and early winter, when detrital coverage was at its maximum, compared to periods when there was no coverage (Kaufmann and Smith, 1997). Either the holothurians were not having to forage so thoroughly for phytodetritus when aggregates were abundant, or they were searching for different kinds of food at different times of the year.

4.7 Summary

The benthic biota reacts at a variety of levels and time scales to seasonally pulsed inputs of organic matter. Small organisms, mainly bacteria and protozoans, respond very quickly with biochemically detectable increases in activity. The production of bacterial exoenzymes is often the first obvious benthic response. Seasonal variations in SCOC observed in the Pacific Ocean probably mainly reflect activity by small organisms. Population increases following phytodetritus inputs are reported for bacteria and foraminifera. There is also evidence for seasonal population fluctuations among metazoan meio-, macro- and mega-fauna, although the responses of metazoans are generally less immediate and obvious than those of bacteria and protozoans. Most deep-sea animals reproduce asynchronously throughout the year but some macro- and mega-faunal species exhibit seasonal periodicity in reproductive processes (gametogenesis, vitellogenesis, spawning, larval settlement) that can be plausibly linked to pulsed food inputs. Changes in rates of megafaunal activity and exposure at the sediment surface are also reported. The deep sea is not a single environment and seasonal processes differ in different oceanic settings. At bathyal depths on continental margins, larger size classes (macro- and mega-fauna) may exhibit seasonal changes, while in abyssal open-ocean areas, seasonality is most evident among the smaller organisms, particularly bacteria and protozoans.

5. A Case Study of Deep-Sea Seasonality

A detailed interdisciplinary investigation (“Project Sagami”), carried out at a bathyal site (St. SB; 1430 m depth) in the central part of Sagami Bay (Japan) from 1996 to 1999, provides a good example of seasonality in deep-sea bentho-pelagic coupling. This site has been sampled for benthic foraminifera since 1991 using a box corer and multicorer (Kitazato and Ohga, 1995; Ohga and Kitazato, 1997). Since 1996, surface primary production, indicated by ocean colour changes and chlorophyll *a* concentrations, have been monitored using the Japanese sea colour observation satellite ADEOS and fluxes through the water column using sediment traps deployed at 350 m and 20 m above the bottom. In addition, the density and behaviour of suspended organic particles near the sediment surface have been observed in video images from an *in situ* seafloor laboratory, situated at a 1174 m depth off Hatsushima Island (Momma *et al*., 1998; Yamaoka *et al*., 1998; Kitazato *et al*., 2000). These records indicate that the density of suspended particles was greatest in the spring, with dense clouds first appearing about 10 days after the start of the spring bloom at the sea surface. The clouds were associated with the deposition of a fluffy layer of phytodetritus on the seafloor. This deposit changed in thickness and distribution on a daily basis (Yamaoka *et al*., 1998).

Processes occurring during 1997/98 at this eutrophic, continental margin site were studied in detail by Kitazato *et al*. (2000) (Fig. 5). The spring bloom occurred between February and April. Water column fluxes were high throughout the year, but high δ^{13}C values and low C/N ratios during March to mid-April indicate that the sinking material was less degraded during this period than at other times of the year. A dense bottom nepheloid layer appeared in March, about 10 days after the beginning of the spring bloom, and persisted until the end of April at the rather shallower seafloor laboratory site. During this period, a phytodetritus deposit composed of light-green aggregates appeared on the seafloor. At Stn. SB, a similar deposit was present between April and June 1997 and chloroplastic pigment (CPE) values were also high. Total organic carbon values in upper sediment layers peaked in June. The thickness of the oxygenated layer of sediment also varied seasonally and was thinnest in May/June, following phytodetritus deposition.

Benthic foraminifera exhibited changes that correspond to this seasonal deposition of organic matter (Kitazato *et al*., 2000). 1) Total standing stocks increased, although, for reasons that are unclear, the increase began just prior to the onset of phytodetritus deposition. 2) Some epifaunal species (*Bolivina pacifica*, *Stainforthia apertura*, *Textularia kattegatensis*) migrated up to colonise the phytodetrital layer where they underwent rapid increases in population densities. 3) Some infaunal species (e.g. *Globobulima afffinis*) also respond to phytodetritus input, albeit to a lesser extent than the epifaunal “phytodetritus species”.

Between December 1996 and August 1998, the central Sagami Bay site was sampled 15 times (average interval 1.4 months) for metazoan meiofauna and sediment parameters using a multiple corer (Shimanaga and Shirayama, 2000; Shimanaga *et al*., 2000). A slight but

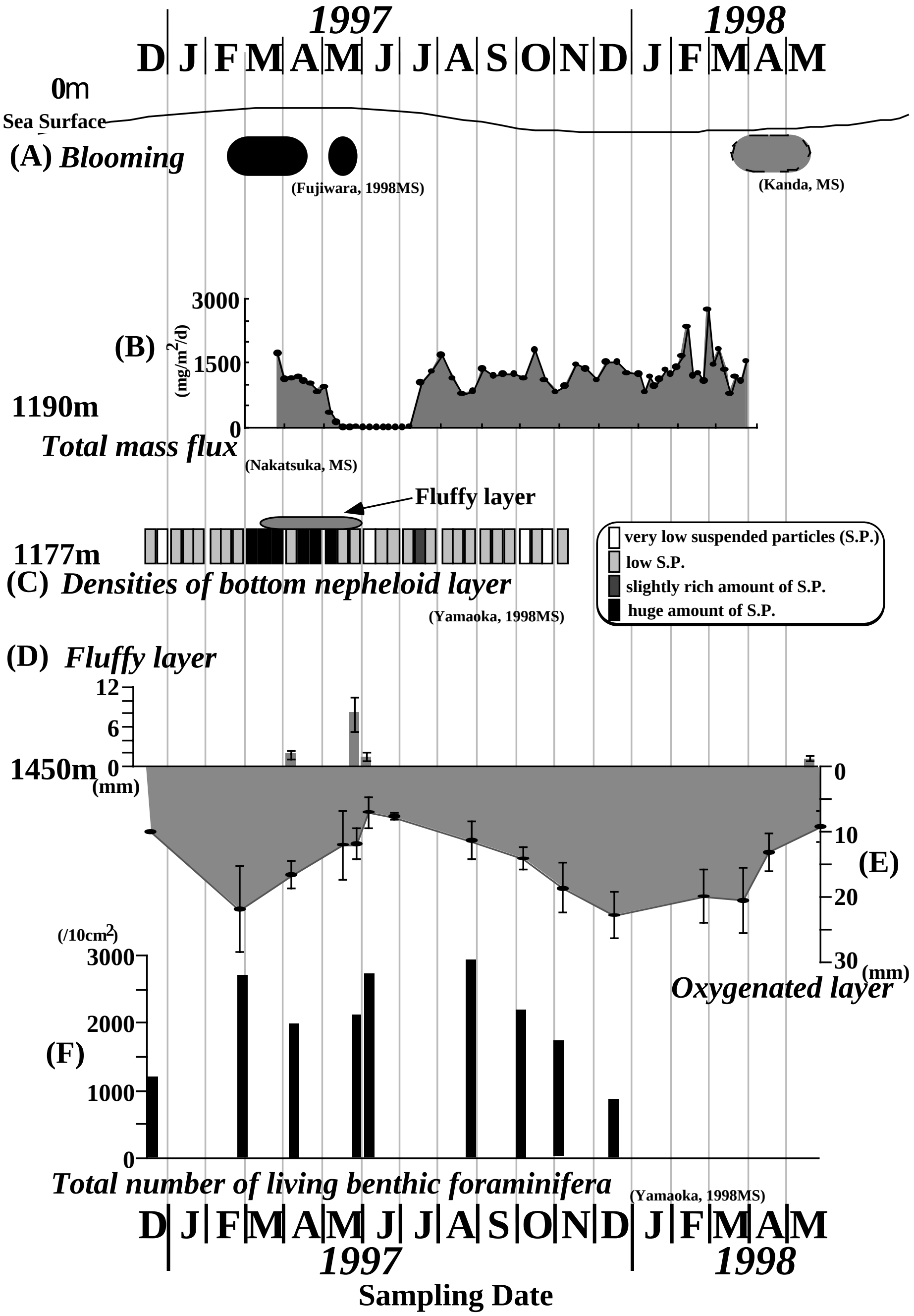

Fig. 5. Summary of results of "Project Sagami" showing seasonal fluctuations in benthopelagic coupling in bathyal Sagami Bay, Japan. A) Spring bloom observed at ocean surface by satellite. B) Changes in total mass flux recorded by sediment traps (low values during May and early June probably due to malfunction). C) Concentration of suspended material in bottom nephaloid layer observed by video at long-term observatory off Hatsushima Island (1177 m water depth). D) Changes in thickness of phytodetritus layer on sediment surface at Stn. SB (1430 m water depth). E) Changes in thickness of oxygenated sediment layer at Stn. SB. F) Changes in total number of rose-Bengal stained foraminifera at Stn. SB. Reprinted from *Mar. Micropaleo.*, **40**, H. Kitazato, Y. Shirayama, T. Nakatsuka, S. Fujiwara, M. Shimanaga, Y. Kato, Y. Okada, J. Kanda, A. Yamaoka, T. Masuzawa and K. Suzuki, Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay: preliminary results from "Project Sagami 1996–1999", figure 1, p. 2741, © 2000 Elsevier Science Ltd, with permission from Elsevier Science.

significant seasonal increase (factor of 1.6) in bacterial densities occurred during the summer, but there was no corresponding increase in metabolic activity (measured as adenylate energy charge) (Shimanaga and Shirayama, 2000). As in other areas (e.g. Pfannkuche, 1993; Drazen *et al*., 1998), metazoans responded less obviously to phytodetrital inputs than the foraminifera. Weak seasonal fluctuations, corresponding to peaks in CPE values, were observed for total meiofauna and nematodes, but these were not significant (Shimanaga and Shirayama, 2000). However, Shimanaga *et al*. (2000) reported that copepods and kinorhynchs (but not nematodes, polychaetes or ostracods) underwent seasonal changes in their vertical distribution, being located closer to the sediment surface when CPE values (reflecting seasonal inputs of labile organic matter) were higher. Like some foraminifera, these taxa apparently migrate upwards in the sediment profile in search of food. Their distributions were not related to shifting oxygen profiles. Ovigerous female copepods and nauplii also exhibited seasonal changes in their vertical distribution patterns, although these changes were not correlated with CPE values. Both occurred at shallower depths in the sediment during May 1998 compared with February 1997. Nauplii were also shallower during June 1997. Shimanaga *et al*. (2000) suggest that copepods reproduce seasonally following pulses of phytodetritus, leading to a lagged increase in the numbers of nauplii and egg-bearing females.

The results of “Project Sagami” are consistent with earlier studies in suggesting that foraminifera are generally more responsive to phytodetrital pulses than meiofaunal metazoans. They also demonstrate that seasonal fluctuations in benthic biota may be more subdued on eutrophic continental margins, where food is reasonably plentiful, than in severely food-limited oligotrophic, open ocean areas.

6. Concluding Remarks

The ocean floor is a major sink for organic carbon. In open ocean areas, much of this material arrives during episodic flux events that recur with a more or less regular seasonal periodicity. These probably represent the most important seasonal signal arriving at the ocean floor. Pulsed inputs of organic matter, and benthic organism responses to them, are of profound importance for understanding the biogeochemical cycling of carbon in the oceans (e.g. papers in Ducklow and Harris, 1993; Eglinton *et al*., 1995), and the generation of the palaeoceanographic record (Graf *et al*., 1995). As in shallow-water systems (Graf, 1992), benthic responses are most evident among smaller organisms, at least over short time scales. Bacteria produce exoenzymes and, following a time lag, start dividing. Protozoans exhibit responses in terms of physiology, feeding and population growth. Metazoan meiofaunal responses are generally more subdued, at least at the major taxon level, while macro- and mega-faunal populations often show no obvious increase in abundance or biomass following pulses of phytodetritus. Alterations in megafaunal behaviour are reported, however, and in a few species, synchronous reproduction or the recruitment of planktotrophic larvae appears to be linked to seasonal food inputs.

The deep seafloor, however, is not a single homogeneous environment and these generalisations do not apply everywhere. In particular, there are strong contrasts between biological processes operating along the edges of the ocean basins (the bathyal continental margins) and the central abyssal regions. Seasonal changes in macro- and mega-faunal densities are reported from continental slopes (Cartes, 1998; Sorbe, 1999). Most examples of seasonal reproduction and recruitment are from bathyal depths, mainly on western Mediterranean and NE Atlantic margins and there are few if any records from truly abyssal settings (Table 2). Some seasonally-reproducing species have ranges extending onto the continental shelf and can hardly be considered as deep-sea taxa (Gage *et al*., 1986). In contrast, benthic responses to pulsed fluxes in abyssal, open ocean areas mostly concern smaller organisms such as bacteria and protozoa. These oligotrophic regions are severely food limited even for bacteria (Turley, 2000), and the level of these inputs is presumably insufficient to fuel population-level or reproductive responses among larger animals. Seasonal processes are by no means a ubiquitous feature of deep-sea ecosystems. Any such paradigm would probably prove as flawed as earlier generalisations (Eckelbarger and Watling, 1995). There are plenty of examples of non-seasonal benthic processes, particularly at abyssal depth. Views of the Madeira Abyssal Plain seafloor taken over a period of a year or more using a time-lapse camera systems reveal an unchanging scene with no indication of pulsed phytodetrital inputs, despite evidence for seasonal flux peaks in the water column (Rice *et al*., 1994). In the same area, the xenophyophore *Reticulammina labyrinthica* exhibited episodic growth with a two-month periodicity which bore no apparent relation to any seasonal cycle (Gooday *et al*., 1993). Elsewhere in the Atlantic, SCOC measurements do not exhibit clear seasonal patterns (Sayles *et al*., 1994) and seasonal changes in metazoan population densities are often not apparent (Pfannkuche, 1993; Gooday *et al*., 1996). Many deep-sea invertebrates are continuous rather than seasonal breeders.

As with other aspects of deep-sea ecology (Gage, 1991), no single paradigm can encompass temporal processes on the ocean floor. Moreover, the intensity of the flux, and the nature of any benthic response, vary from year to year and discrepancies occur between the food supply and demand; i.e. between POC flux and SCOC. In the deep sea, as in other habitats (e.g. Jackson *et al*., 2001), long-term studies are essential in order to understand better how benthic systems behave on ecological time scales. Because of funding and logistic constraints, there have been relatively few such studies, and most of these have been carried out have been conducted at continental margin sites that can be easily visited on a regular basis by research vessels (Table 1). In open ocean areas far from land, sediment trap mooring can be used to document fluxes and time-lapse camera systems to monitor the activities of benthic megafauna in relation to phytodetritus inputs over long time periods. However, it is usually impossible to sample the benthic community at the right time, or with sufficient and sustained frequency, to document short-term responses to flux events in these remote settings. These problems must be overcome if our knowledge of temporal phenomena central oceanic areas is to be improved.

One final point to emphasise is that seasonal organic matter inputs make an important contribution to the spatial heterogeneity of the ocean-floor environment. In practice, it is often difficult to distinguish between temporal variability and spatial patchiness without examining a large number of replicate samples from different seasons. Small-scale heterogeneity is widely regarded as one of the important factors underlying high levels of local (alpha) benthic diversity in the deep sea (e.g. Grassle and Morse-Porteous, 1987; Snelgrove *et al*., 1992, 1994, 1996; Smith, 1994). The complex interactions between the physical irregularity of the seafloor, bottom-water hydrography, the activities of benthic organisms, and organic matter inputs which vary over time, need to be considered in any explanation of high local species diversity.

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