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A benthic foraminiferal proxy of pulsed organic matter paleofluxes

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Abstract

In the temperate open ocean of the modern northeast Atlantic, the spring bloom of phytoplankton leads to a seasonal pulse of detrital organic material (phytodetritus) to the ocean floor. Opportunistic benthic foraminifera rapidly colonise this food resource, producing large numbers of individuals whose tests are ultimately added to the sediment. One of these taxa, *Epistominella exigua*, shows periodic peaks in abundance in the fossil record at many open ocean sites. Previously, such peaks have been commonly interpreted to result from changes in physicochemical properties of bottom water mass and thus deep-sea circulation. The main purpose of this paper is to propose that *E. exigua* may be used as a proxy of pulsed organic matter inputs to the deep ocean and therefore as an indicator of relative changes in productivity.

1. Introduction

Foraminifera dominate modern ocean-floor meiobenthic and macrobenthic communities (Gooday et al., 1992) and are also the most abundant benthic deep-sea organisms preserved in the fossil record. The environmental factors which influence their distribution and abundance on the ocean floor are complex and controversial but may include bathymetry, sediment type, the physicochemical character of bottom water masses (including degree of calcium carbonate saturation and oxygenation) and surface productivity (Streeter, 1973; Schnitker, 1980; Douglas and Woodruff, 1981; Bremer and Lohmann, 1982; Lutze and Coulbourn 1984; Murray, 1991). Recent studies have emphasised the strong influence that organic matter inputs, particularly those originating from surface production, exert on deep-sea benthic foraminiferal communities (Caralp, 1984, 1989; Lutze and Coulbourn, 1984; Altenbach and Sarnthein, 1989; Loubere, 1991).

Like that of other deep-sea biota (Rowe, 1983; Sibuet et al., 1989), foraminiferal biomass is closely related to the amount of organic matter (food) reaching the ocean floor. Thus, the overall abundance of benthic foraminifera can be used to provide an estimate of paleoproductivity (Herguera and Berger, 1991). Distinctive species assemblages are typically found in areas where organic matter inputs are high. For exam-

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ple, Lutze and Coulbourn (1984), Lutze et al. (1986) and Mackensen et al. (1993) identify "high productivity groups" of species associated with areas of high primary productivity along continental margins. Distinctive assemblages also flourish in areas where the oxygen minimum zone impinges on the continental slope (e.g. Hermelin and Shimmield, 1990). These populations are dominated by species able to withstand low oxygen concentrations (Bernhard, 1992; Murray, 1991) and with test morphologies indicative of an infaunal life-style (Corliss and Chen, 1988). Similar associations have been inferred to exist in fossil material (Bernhard, 1986) and have been used to interpret the paleoceanographic record (e.g. Bernhard, 1986; Lutze et al., 1986; Caralp, 1989; Thomas, 1990; Gooday, 1993). In a biological sense, the close link between foraminiferal populations and organic matter inputs is most probably related to the "simple" organisation of these protists and their consequent ability to respond to, and rapidly utilize, food material (Altenbach, 1992; Gooday et al., 1992; Linke, 1992).

As shown above, these relationships are well studied in modern sediments in marginal oceanic settings. Less is known about linkages between benthic foraminifera and nutrient fluxes in well oxygenated, open ocean sediments. In an elegant study, Loubere (1991) demonstrated progressive changes in modern species assemblages along a transect in the eastern equatorial Pacific, a central oceanic area where surface productivity is the only environmental parameter that changes. Recent biological research in the northeast Atlantic has demonstrated an association between seasonal pulses of organic matter (phytodetritus) and certain foraminiferal species (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Thiel et al., 1989). Unlike the "high productivity/low oxygen" taxa referred to above, these "phytodetritus species" typically have spiral test morphologies indicative of an epifaunal mode of life (Corliss, 1985; Corliss and Chen, 1988). The purpose of this paper is to explore the hypothesis that such species can serve as proxies for phytodetrital inputs in Quaternary and Neogene oceanic sediments, and to encourage others to test this hypothesis.

2. Associations between benthic foraminifera and phytodetritus

Phytodetritus was first described from the deep-sea by biologists at the Institute of Oceanographic Sciences Deacon Laboratory (Billett et al., 1983; Rice et al., 1986; Thiel et al., 1989). It consists of phytoplankton and zooplankton remains, bound together in a gelatinous matrix to form aggregates up to about one centimetre. These originate in the euphotic zone during the spring bloom (and probably in smaller amounts at other times of the year), and settle over a period of weeks through the water column to form a patchy deposit of light fluffy material on the ocean floor. This material is present in large quantities only during the spring and summer, and thus represents an essentially seasonal pulse of food for the deep-sea benthos. The deposition of phytodetritus is well documented at bathyal and abyssal depths in the northeast Atlantic as well as other areas (Gooday and Turley, 1990).

Aggregates of phytodetritus are colonised by benthic foraminifera. In abyssal samples, two calcareous species, *Epistominella exigua* and *Alabaminella weddellensis* (in addition to the allogromiid *Tinogullmia riemanni*) are dominant (Gooday, 1988). At bathyal depths, the dominant species is *Epistominella pusilla* (Gooday and Lambshead, 1989). Phytodetritus provides a food source for these species and controls their population dynamics (Gooday and Lambshead, 1989; Gooday and Turley, 1990). During the summer, many live individuals occur within the aggregates, but relatively few are found in the underlying sediment. During the winter and early spring, when phytodetritus is absent from the sea floor, population levels are much lower. *E. exigua* and *A. weddellensis* are probably opportunistic species which grow and reproduce rapidly. They are both characterised by small test size, smooth, transparent test walls, and epifaunal (spiral) test morphologies (Gooday and Lambshead, 1989). Calcareous foraminifera inhabiting the phytodetritus are almost invariably small. *Alabaminella weddellensis* ranges from 60 to 180 μm, *Epistominella pusilla* from 30 to 170 μm and *E. exigua* is usually <200 μm in diameter, although a few specimens exceed 300 μm (Gooday, 1993). A minute, undescribed *Fursenkoina* species, which is fairly common in abyssal phytodetrital samples, measures 40–130 μm in length (size histograms of these species are given in Gooday, 1993). These small opportunistic species are retained on fine (63 μm or 31 μm) sieves and would be missed in studies utilizing coarser size fractions (e.g. Schröder et al., 1987).

3. Material and methods

RRS *Charles Darwin* Cruise Leg 138 recovered Core 38-02 from the northern edge of the Nazca Ridge in the Pacific Ocean (15° 57.26'S, 77° 04.36'W, present water depth 2530 m) (Fig. 1). A detailed δ^{18}O record for Core 38-02 indicates that a complete sequence exists to the end of δ^{18}O Stage 8, approximately 270,000 yrs BP.

The δ^{18}O stratigraphy was based on *Neogloboquadrina dutertrei* (150–200 μm) from Core 38-02 (Fig. 2). The samples were analyzed on a VG Isotech PRISM mass spectrometer by Cartlidge and Corfield at Oxford University. Each analysis was typically performed on 40 specimens, although constant results were obtained from samples of fewer than five individuals.

The Atlantic results are based on five Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites: Site 400A (Bay of Biscay, 47°22.90'N, 09°11.90'W, present water depth 4399 m); Site 518 (Rio Grande Rise, 29°58.42'S, 38°08.12'W, 3944 m); Site 529 (Walvis Ridge, 28°55.83'S, 02°46.08'E, 3035 m); Site 563 (west of mid-Atlantic Ridge, 33°38.53'N, 43°46.04'W, 3786 m); and Site 667A (Sierra Leone Rise, 04°34.15'N, 21°54.68'W, 3529 m) (Fig. 1).

Data for the Miocene to Recent from the eastern equatorial Pacific were obtained from DSDP Sites 572 (01°26.09'N, 113°50.52'W, present water depth 3893 m) and 573 (00°29.91'N, 133°18.57'W, 4301 m) (Fig. 1). Data for Site 573 were published in Thomas (1985); data for Site 572 were obtained by Thomas during DSDP Leg 85, but not published.

For the faunal analyses, benthic foraminifers were picked from the >63 μm size-fraction to ensure that the large number of small-sized specimens were included in the analysis. No attempt was made to collect data on the absolute abundance of benthic foraminifera, because this is based on the assumption of uniform sedimentation rates over long periods of time. In modern assemblages, an increase in the absolute abundance of a "phytodetritus species" is matched by an increase in its relative abundance (e.g. Gooday and Lambshead, 1989).

4. Results

In order to illustrate the possible influence of phytodetritus on fossil foraminiferal faunas, we focus on three case studies, one from the Upper Quaternary of the Southwest Pacific, one from the Atlantic Miocene, and one from the Pacific Neogene. We consider one species, *Epistominella exigua*, because it is the best known of the phytodetritus-exploiting species, having an almost cosmopolitan distribution in the modern world ocean (Murray, 1991) and a well documented fossil record extending back to the middle Eocene (Thomas, 1990, 1992; Boltovskoy and Boltovskoy, 1989; Boltovskoy et al., 1992). It is probably the most abundant calcareous foraminiferal species in the deep late Neogene North Atlantic (Murray, 1984; Lukashina, 1988). However, our conclusions should also apply to abundant but less well known species *Alabaminella weddellensis*, which commonly co-occurs with *E. exigua* (see for example Thomas, 1986, figs. 3 and 4). In order to document these small foraminifera, it is necessary to examine fractions >63 μm, as in the present study.

4.1. Upper Quaternary of Nazca Ridge

Among the diverse benthic foraminiferal assemblages recovered from these sediments, there

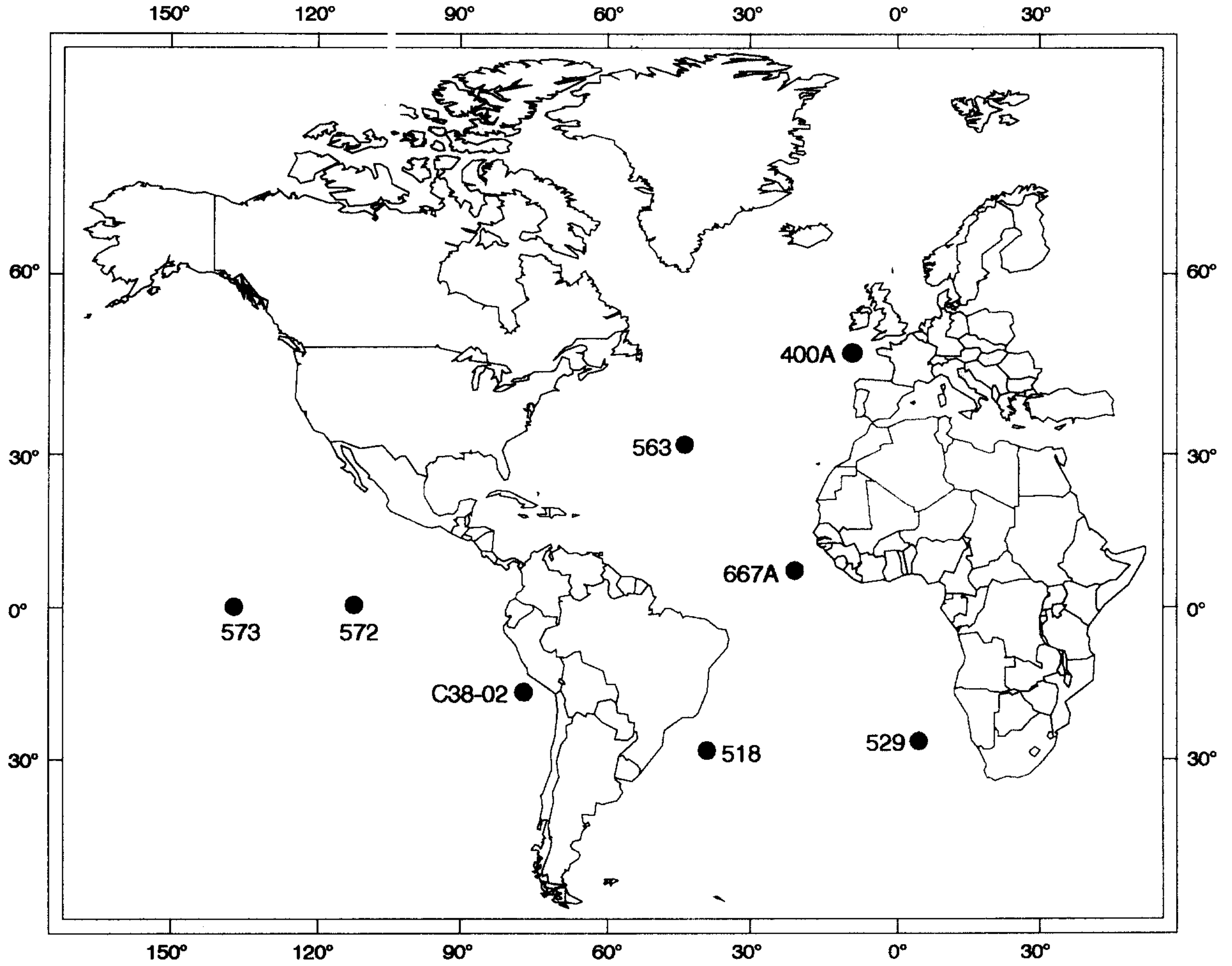

Fig. 1. Map showing location of DSDP and ODP Sites and Quaternary RRS *Charles Darwin* Cruise Site (C38-02).

is a clear negative correlation between the relative abundance of *E. exigua* and that of *Uvigerina peregrina*, a species with an infaunal test morphology (Fig. 2). Relative abundances of *E. exigua* decrease upsection, with marked falls during the middle of δ^{18}O glacial Stage 6 (~470 cm) and interglacial Stage 5. *U. peregrina* increases above the middle of δ^{18}O Stage 5 (~300 cm) to become most abundant during the Holocene. *E. exigua* is insignificant above δ^{18}O Stage 5, although there is a small increase in the Holocene.

4.2. The Atlantic Miocene

From this study, the Miocene benthic foraminiferal assemblages from the Atlantic Ocean are diverse. The temporal changes in relative abundance of *E. exigua* are plotted versus nannofossil zones [400A: Müller (1979); 518: Berggren et al. (1983); 529: Jiang and Gartner (1984); 563: Miller et al. (1985); 667A: Manivit (1989)] (Fig. 3). The percentages of *E. exigua* fluctuate greatly at the five sites, typically varying from 5% to 20% or more (Fig. 3). At Site 400A, located

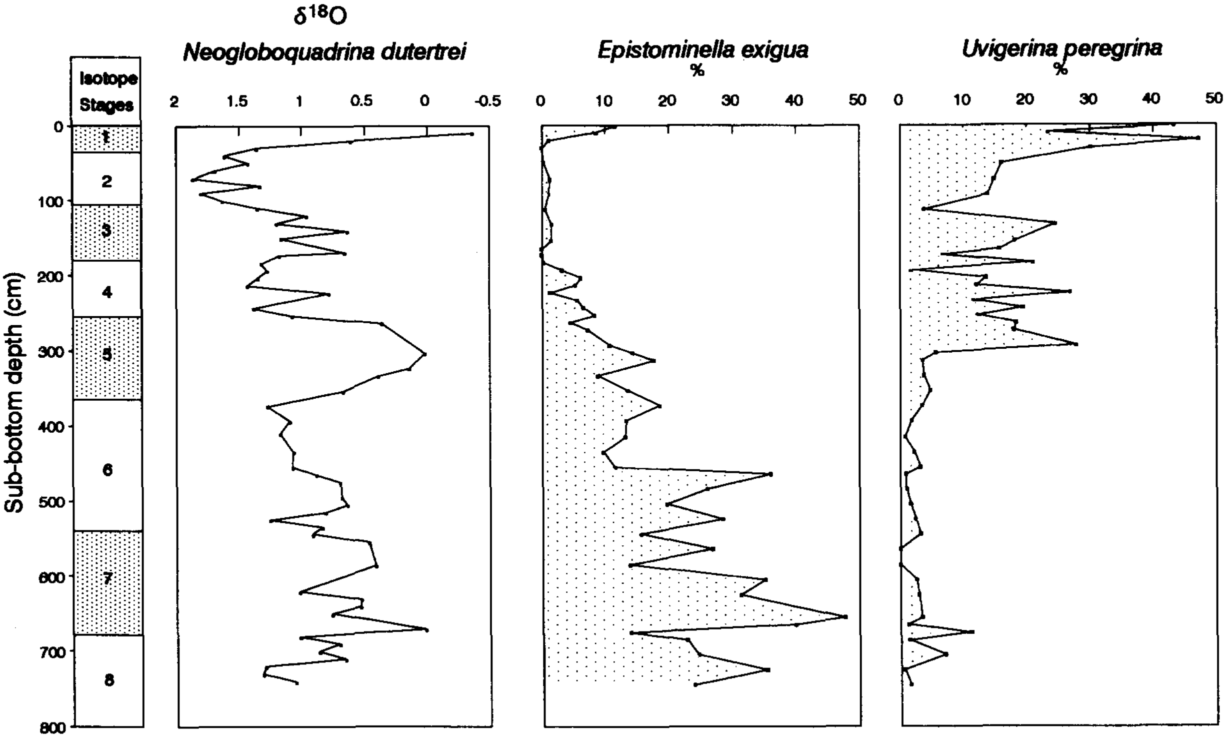

Fig. 2. Fluctuations in the relative abundance of *Epistominella exigua* and *Uvigerina peregrina* plotted versus sub-bottom depth (cm) and Isotope Stages during the Quaternary in Core 38-02. Also shown is the *Neogloboquadrina dutertrei* $\delta^{18}O$ curve. Stippled areas (odd numbers) in Isotope Stages are interglacial periods and non-stippled areas (even numbers) are glacial periods.

on the northern margin of the Bay of Biscay in an area of present-day phytodetritus production (Gooday and Turley, 1990), the variation is even more dramatic (from 0 to nearly 40%). This contrasts with the relatively modest fluctuations (5–18%) in an area of the North Atlantic (Site 563) which at present experiences low surface primary productivity under a central oceanic gyre (Berger, 1989). Taking the Atlantic as a whole, there is no apparent stratigraphic correlation of abundance peaks of *E. exigua* between sites during the Miocene (see Fig. 3).

4.3. The eastern equatorial Pacific: Miocene–Recent

Temporal changes in relative abundance of *E. exigua* are plotted versus numerical time (Barron et al., 1985) (Fig. 4). Strong variations in relative abundance of *E. exigua* occur, with higher maximum values at the more eastern Site 572, which is closer to the area of equatorial upwelling in the eastern Pacific. There is no obvious correlation between the timing of all the peaks at the two sites. The largest peak at Sites 572 and 573 occur at 9–10 Ma, and these peaks appear to be coeval with occurrences of laminated diatom oozes at the same sites, inferred to indicate periods of increased primary production (9.9–10.5 Ma, Kemp and Baldauf, 1993). Lesser peaks at about 6 Ma may be coeval with such periods as well, but they are not as clearly defined. The *E. exigua* peaks, however, differ in duration (9–12 Ma at Site 573 versus 8.5–9.5 Ma at Site 572 for the largest peaks) as far as can be ascertained from the data, whereas the diatom occurrences are said to be coeval from site to site (Kemp and Baldauf, 1993). More recently, work from Site 844, eastern equatorial Pacific (ODP Leg 138) has shown a negative correlation between the relative abundance of *E. exigua* and

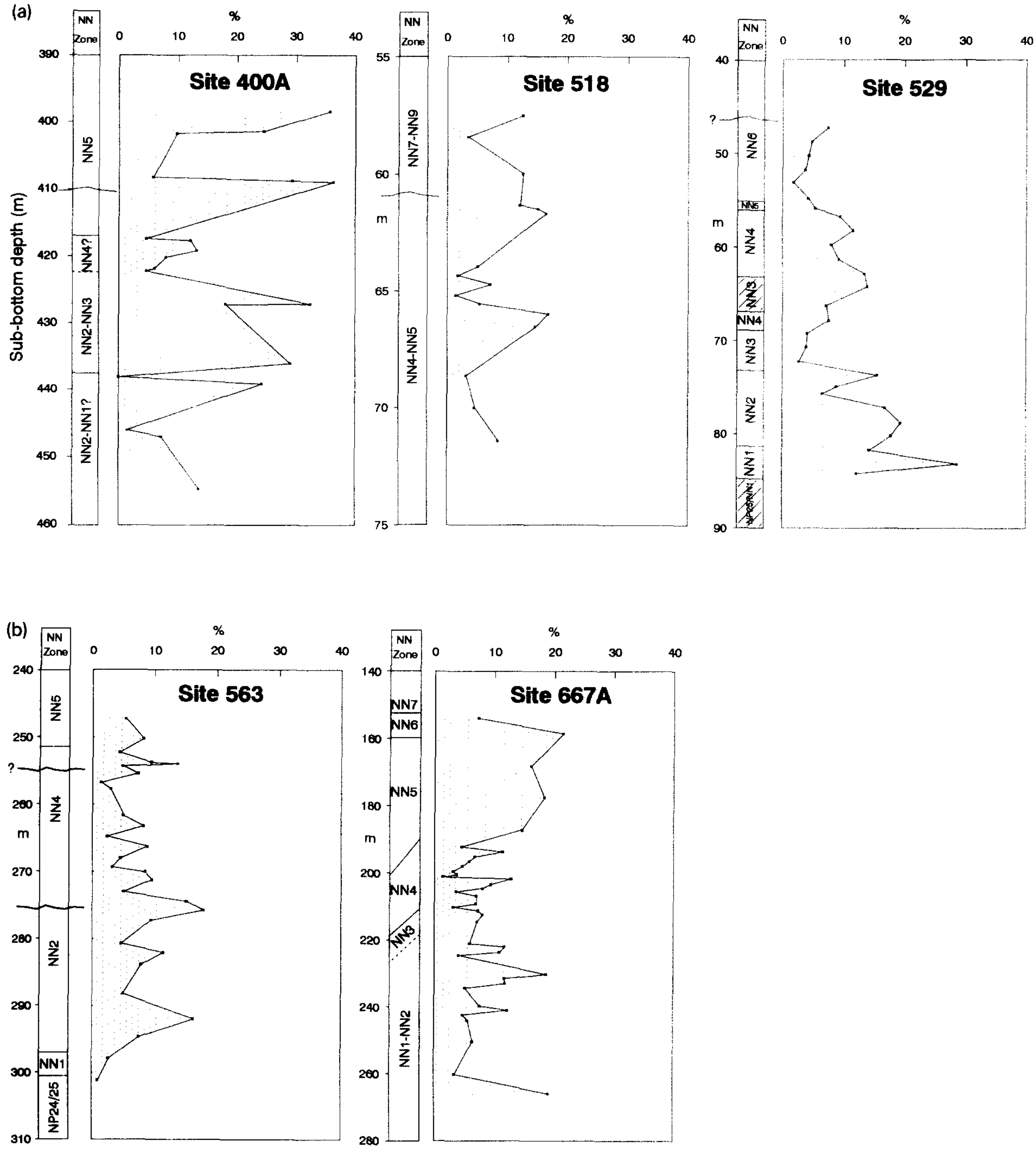

Fig. 3. Fluctuations in the relative abundance of *Epistominella exigua* plotted versus sub-bottom depth (m) and nannofossil zonation during the early to middle Miocene at the Atlantic Sites. *NN Zone* = Nannofossil zone; wavy lines show positions of hiatuses; shaded areas in NN Zone of Site 529 indicate slumping.

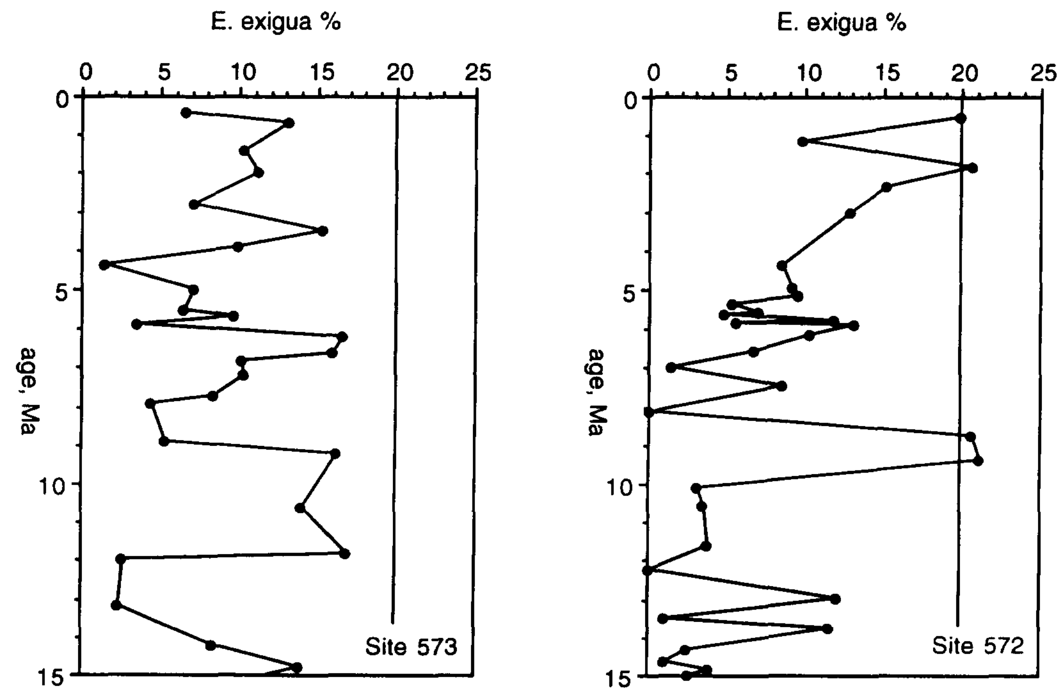

Fig. 4. Fluctuations in the relative abundance of *Epistominella exigua* plotted versus numerical time from the Miocene to Recent at Sites 572 and 573, eastern equatorial Pacific. Age control is after Barron et al. (1985).

the occurrence of laminated sediments (King et al., in press).

5. Discussion

Patterns of relative species abundances, similar to those we observe in the Upper Quaternary of the Nazca Ridge, have been reported from the North Atlantic. Here, associations between *U. peregrina* and glacial sediments have been documented by several authors (Corliss et al., 1986, p. 1114). Schnitker (1974, 1980) found that in both modern and interglacial sediments, *E. exigua* (>125 μm) is the dominant species in the deep basins of the NW Atlantic, with *U. peregrina* being restricted to relatively shallow areas along the continental margin and the crest of the Mid-Atlantic Ridge. During the last glacial period, *U. peregrina* became the dominant species in the northern basins and *E. exigua* became displaced southwards. In >150 μm residues from a piston core recovered from the Mid-Atlantic Ridge, *U. peregrina* was dominant during glacial periods and varied in abundance inversely with *E. exigua* (and *Cibicides wuellerstorfi*) (Streeter and Shackleton, 1979). According to Murray et al. (1986), *E. exigua* (>125 μm) was more abundant during interglacials than during glacials in the northeast Atlantic. Finally, Thomas et al. (1992) found that in Core 5K from the northeast Atlantic, *E. exigua* and *Eilohedra* (=*Alabaminella*) *weddellensis* (>63 μm) increased rapidly in relative and absolute abundances to dominate foraminiferal assemblages after deglaciation. Only this latter study, which is based on fractions >63 μm, provides results directly comparable to ours.

A number of authors (Streeter, 1973; Schnitker, 1974, 1979, 1980; Weston and Murray, 1984; Gaydyukov and Lukashina, 1988) have linked the distribution of *E. exigua*, or biofacies characterized by this species, to "young", well oxygenated bottom water (Northeast Atlantic Deep Water) (Gooday, 1993). This apparent relationship has been used to infer past changes in deep water mass circulation (Schnitker, 1974, 1980). For example, Murray (1988) plotted progressive changes through time in the northeast Atlantic distribution of three biofacies derived by *Q*-mode factor analysis of modern samples (>125 μm). Factor 3, dominated by *E. exigua* and representing Northeast Atlantic Deep Water (NEADW), underwent a dramatic increase in abundance and distribution at the end of the Pliocene. Murray (1988) interpreted these changes in terms of an increased production of NEADW resulting from circulation changes coincident with the onset of Northern Hemisphere glaciation. Increases in the abundance of *E. exigua* (>63 μm and >150 μm) in the early Miocene to early Pliocene of the Pacific Ocean have been linked also to the development of bottom water masses, particularly Pacific Bottom Water (Kurihara and Kennett, 1985; Woodruff, 1985).

There appears, however, to be no consistent relationship between *E. exigua* and deep water hydrography (Braatz and Corliss, 1987; Gooday, 1993). For example, in the northeast Atlantic alone, *E. exigua* occurs in areas overlain by water which ranges in temperature from −1°C to 10°C (Murray, 1991, p. 158). Modern *E. exigua* is found living in phytodetritus (Gooday and Lambshead, 1989) but the fossil occurrences discussed here are from too great a water depth to show the presence of *A. weddellensis*. We therefore favour the view that fluctuations in the abundance of *E. exigua* with time reflect variability in the production of phytodetritus. This process occurs in the euphotic zone and is linked to the hydrographic structure of the upper water column, particularly the depth of the winter mixed layer (Gooday, 1993). According to this interpretation, the abundance of at least some deep-sea benthic foraminiferal species depends on the nature of the immediately overlying water column rather than the characteristics of bottom water masses derived from geographically distant high latitude sources. Thomas et al. (1992) have already suggested that the increase in relative abundances of *E. exigua* and *A. weddellensis* following the last deglaciation in the northeast Atlantic was linked to a highly increased input of phytodetritus. Similarly, Mackensen (1992) related an uppermost Miocene and Pliocene assemblage (>125 μm) characterized by *E. exigua* from the southern Indian Ocean to high biosiliceous productivity leading to phytodetritus sedimentation.

If this view is correct, then populations of opportunistic, epifaunal species such as *E. exigua* may represent a proxy for seasonal pulses of phytodetritus originating from surface primary productivity in open ocean eutrophic areas. Although a single seasonal input of phytodetritus would leave no trace in the fossil record, it is possible to speculate on the broad response of *E. exigua* and similar species to increasing or decreasing inputs over many years. We believe that inputs added over a geologically significant period of time are documented by *E. exigua* peaks. Thus, fluctuations in the abundances of phytodetritus-exploiting species through time may be used as indicators of local variations in surface productivity. A good example is provided by the differences in magnitude of *E. exigua* peaks during the Miocene at Site 400A (0–40%) and Site 563 (5–18%), which are located in the modern phytodetritus zone and in an oligotrophic area respectively. We interpret these differences to mean that the general productivity patterns during the Miocene were similar to those operating in the modern North Atlantic.

6. Conclusions

The main purpose of this paper is to propose that *E. exigua* may be used as a proxy of pulsed organic matter inputs to the deep ocean and therefore as an indicator of relative changes in productivity. It is important to note that *E. exigua*, and other opportunistic phytodetritus-exploiting species, often have small tests which are adequately retained only on fine (63 μm) mesh sieves. We believe that variations in phytodetritus flux may explain some of the changes in *relative* abundances of *E. exigua* observed in the Miocene and Quaternary deep-sea sections which we have studied. These patterns need to be confirmed by studies that establish similar variations in *absolute* abundances.

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