Modern Nereites in the South China Sea—Ecological Association with Redox Conditions in the Sediment

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INTRODUCTION

The suitability of trace fossils and ichnofabrics as ecological indicators improves where modern analogs provide additional information about the habitat of the fossil counterparts (e.g., Bromley, 1996). This paper provides new observations about the trace fossil Nereites from modern deep-sea environments.

Nereites and related trace fossils are very common in the fossil record (for taxonomic revision of the Nereites-Scalarituba-Helminthoida group, see Uchman, 1995). Very old Neonereites have been reported from Dalradian (Neoproterozoic) shallow-water deposits from Scotland by Brasier and McIlroy (1998) and from Cambrian shallow-water sediments (e.g., Crimes and Anderson, 1985). Nereites is most commonly reported from turbidite sequences. Examples have been described by Orr (1995; Ordovician-Silurian, Wales; 1994: Carboniferous, Spain), Crimes and Crossley (1991: Silurian, Ireland), Chamberlain and Clark (1973) and Ekdale and Mason (1988; Pennsylvanian-Permian, U.S.A, using the name Scalarituba), Seilacher (1962: Cretaceous-Tertiary, Spain), Macerat (1967: Tertiary, Venezuela), Książkiewicz (1977: Tertiary, Poland), Uchman (1995: Tertiary, Italy; 1999: Cretaceous, Germany and Austria), and Uchman and Demircan (1999: Tertiary, Turkey). For some turbidite sequences (flysch) that formed during the Alpine tectonic cycle, the trace fossil Helminthoida (now grouped into the ichnogenus Nereites; Uchman, 1995) is eponymous; the so-called Helminthoida Flysch occurs in Switzerland, France, and Italy (e.g., Triumpy, 1980; Sagri, 1980; Homewood, 1983; Powichrowski, 1989).

Because of its frequent occurrence, Seilacher (1967) introduced the Nereites ichnofacies as a recurrent type of trace fossil community in deep-marine, turbidite-affected settings. Later, Frey and Pemberton (1984, p. 193) defined the environment for the Nereites ichnofacies as “bathyal to abyssal, mostly quiet but oxygenated waters, in places interrupted by down-canyon bottom currents or turbidity currents (flysch deposits); or highly stable, very slowly accreting substrates. In flysch or flysch-like deposits, pelagic muds typically are bounded above and below by turbidites. In more distal regions, the record is mainly one of continuous deposition and bioturbation. (The stable deep-sea floor is not universally bioturbated, however, at least not equally intensely at every site).”

The Nereites ichnofacies is typical for deep-marine settings. However, trace fossils belonging to the ichnogenus Nereites also occur in other environments, such as tidal flats (Mángano et al., 2000), shallow-marine deposits (Schlirf, 2000), and freshwater lakes (e.g., Hu et al., 1998).

In turbidites, Nereites often occurs post-depositionally in the tier just below the surface layer, which implies production at a shallow depth within oxygenated sediment (e.g., Seilacher, 1962; Crimes, 1973; Orr, 1994; Uchman, 1995, 1999; Wetzel and Uchman, 1998), although some deep penetration has been reported (e.g., Seilacher, 1962). In the Recent, the near-surface zone is known for rapid geochemical changes (e.g., Froelich et al., 1979), that cannot be reconstructed easily in the fossil record due to subsequent diagenesis. Therefore, the specific environmental conditions affecting the habitat of the Nereites producer only can be inferred (e.g., Wetzel and Uchman, 1998).

AREA OF INVESTIGATION

The South China Sea is a western marginal sea of the Pacific Ocean. It is surrounded by the Southeast Asian mainland to the north and west (southern part of China, Vietnam, Thailand, Malaysia) and the islands of Borneo, Palawan, Luzon, and Taiwan to the south and east (Fig. 1). It includes large shelf regions and deep basins; the prominent basin between the Philippines and Vietnam is ~4300 m deep. The major connection between the South China Sea and the Pacific Ocean is the Bashi Channel between Taiwan and Luzon, which has a sill depth of about

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FIGURE 1—The South China Sea is a marginal sea of the western Pacific surrounded mainly by shelf areas, as indicated by the 200 m depth contour. The South China Sea is ventilated via the Bashi Channel between the Philippines and Taiwan. The area influenced by upwelling roughly coincides with that affected by wind-stress exceeding 25 cm/d (Wiesner et al., 1996) located roughly westward of the stippled line. Inset represents area shown in Figures 2 and 5.

2600 m (Tomczak and Godfrey, 1994). Bottom waters of the South China Sea are predominantly well oxygenated (ca. 2 ml O$_2$/l; Wyrtki, 1961; Chao et al., 1996) and are introduced via the Bashi Channel.

The oceanographic features of the South China Sea are conditioned by seasonal reversal of the monsoonal wind system. During the SW-monsoon (June–September), pronounced upwelling takes place off central south Vietnam. Forced by the general northeasterly directed surface current flow, the ascending cold and nutrient-rich waters are advected into the central South China Sea (LaFond, 1966). During the NE-monsoon (November–April), upwelling occurs off northwest Luzon and in the southern central South China Sea, where deep water ascends to subsurface depths of 50–100 m and nutrient entrainment is controlled largely by the intensity of wind-induced mixing. The surface-water circulation is counterclockwise, causing the Pacific water to intrude through the Bashi Channel and flow along the coasts to SE Vietnam (Shaw et al., 1986). Along with this seasonal incorporation of nutrients into the euphotic zone, the fluxes of particulate matter to the sea floor off Luzon and Vietnam and in the central South China Sea maximize at the culmination of the SW- and NE-monsoon (Wiesner et al., 1996). During both seasons, about 70% of the total annual organic matter flux is exported to the deep sea (Wiesner et al., 1996). Upwelling in the South China Sea normally enhances the primary production by a factor of 3 to 4 (Antoine et al., 1996), but El Niño events suppress upwelling and lead to a significant reduction in particle flux (Wiesner, 2000, pers. commun.). Periods of high organic matter fluxes are synchronous with periods of intensified wind-induced upwelling and mixing, whereas weak upwelling leads to low organic matter flux. Today the CCD (calcite compensation depth) is located in about 3500 m water depth (e.g., Wang, 1999). Material derived from the Philippines or the adjacent continental slope is transported to the deep sea by turbidites or indistinct downslope transport (e.g., Zhou and Zhao, 1999).

In 1991, ash erupted by Mt. Pinatubo on the Philippines was deposited over an area of about 400,000 km$^2$, forming a layer up to 10 cm thick in the South China Sea (Wiesner et al., 2002; Fig. 2). The ash is an excellent marker bed. On top of the ash is organic-rich fluff that contains 3–5% $C_{org}$ (Wiesner, pers. commun., 2000).

MATERIAL AND METHODS

Samples were collected during several cruises of the German research vessel Sonne to the South China Sea (Sarnthein et al., 1994; Wiesner et al., 1997, 1998, 1999; Fig. 2). They were taken by a 50 x 50-cm$^2$ box corer, which has automatically closing flaps to protect the sediment surface from winnowing during retrieval of the corer. To analyse sedimentary structures in detail, 8-mm-thick sediment slices were prepared for X-ray radiography (Werner, 1967). They were radiated in the laboratory at 30 kV for varying times determined automatically. For three-dimensional analysis of the sedimentary structures, serial sections in vertical and horizontal directions were prepared. Shear strength was measured by using a GEONOR fall-cone apparatus (Hansbo, 1957). Organic carbon was calculated as the difference between total carbon measured on an Erba Science NA 1500 Elemental Analyzer and carbonate carbon measured on a Woesthoff Carmograph 6...
using calcite standards for calibration and 2N $\text{H}_3\text{PO}_4$ for sample acidification. Organic carbon was measured at the Institute of Biogeochemistry and Marine Chemistry of the University of Hamburg.

**OBSERVATIONS ON NEREITES**

The near-surface muds in the deep areas of the central South China Sea display a typical ichnofabric. It consists of tunnels filled by less dense, fine-grained material that is surrounded by sediment enriched in coarse grains compared to the tunnel fill and the host sediment. The coarse envelope displays the characteristics of a reworking halo. The outer boundary of the reworking halo is seldom sharp (Figs. 3, 4). In vertical sections, from the seafloor down to a depth of 3 to 6 cm, tunnels are nearly vertical to inclined, becoming (sub)horizontal. At this level the tunnels adopt a winding course (Figs. 3, 4). The burrows do not cross-cut themselves. On average, the tunnels measure 2 to 4 mm in diameter and the reworking halo is 1 to 2 mm wide. The burrows penetrate up to 9 cm, with an average of 4 to 6 cm. Based on their expression in X-ray radiographs, burrow morphologies match that of *Nereites* missouriensis (Weller, 1899; previously called *Scalarituba missouriensis*, Uchman, 1995).

The ichnogenus *Nereites* comprises a wide variety of winding to meandering traces consisting of an actively filled tunnel enveloped by a halo of reworked sediment. This paper follows the taxonomy provided by Uchman (1995), as slightly emended by Mángano et al. (2000, p. 150), giving the following diagnosis: “Selectively preserved, curved, winding to regularly meandering or spiral, unbranched, predominantly horizontal trails, consisting of a median backfilled tunnel enveloped by an even to lobate zone of reworked sediment.”

This diagnosis lumps *Helminthoida*, *Neonereites*, and *Scalarituba* into the ichnogenus *Nereites* (Uchman, 1995). However, consensus on this taxonomic issue has not yet been reached (Mángano et al., 2000). Uchman (1995) emphasized the importance of a central tunnel enveloped by a zone of reworked sediment as a diagnostic feature (sensu Führich, 1974) of the ichnogenus *Nereites*. The type of preservation should not be used as an ichnotaxon at the ichnogeneric level; hence, *Scalarituba* should be regarded as junior synonym of *Nereites*. Burrow course (meandering vs. non-meandering), width of the central tunnel and envelope zone, nature of the envelope (including shape of lobes), type of preservation, and selective preservation of morphological elements were regarded by Uchman (1995) as accessory features to be used for ichnospecific assignment.

The spatial occurrence of *Nereites* reflects the sediment type to which the *Nereites* producers appear to be adapted. *Nereites* traces are restricted to the central basin of the South China Sea where water depth exceeds 4000 m (Fig. 5; Table 1). Sediments in the basin accumulated below the CCD (e.g., Wang, 1999); hence, the host sediment for the studied *Nereites* is uniformly fine-grained mud. The sediment accumulated at a rate of about 5 to 6 cm/ky (calculated from an accumulation rate of 3.29 g cm$^{-2}$ ky$^{-1}$; Wang, 1999). The *Nereites* host sediment contains about 0.2 to 0.6% $C_{org}$ (Table 1). Porosity of the host sediment varies between 70 and 75%, while undrained shear strength is approximately 0.3 to 1.8 kPa; hence, sediment consistency is classified as soft to soupy. *Nereites* were observed exclusively in brownish sediments. Pore water at the level of the horizontal portion of *Nereites* burrows displays a lowered oxygen content of 25 $\mu$mol O$_2$/L compared to 125 $\mu$mol O$_2$/L of the bottom water (Haacke et al., 2001). *Nereites* occur above a dark-colored zone stained by manganese oxides that rests on top of greenish to gray sediments; the manganese-stained horizon marks the redox boundary (e.g., Froelich et al., 1979). The distance between the manganese-stained horizon and the horizontal part of the burrows is fairly constant in the range of about 1 to 2 cm (Fig. 6). *Nereites* never penetrate into the manganese-stained muds or into the underlying gray to greenish muds.

*Nereites* was not observed in fairly coarse foraminiferal ooze (e.g., cores 419, 420, 955, 956; see Fig. 5) or in sediments that were reworked by bottom currents (e.g., cores 221, 223, 413; see Fig. 5). The latter are stiff sediments with an undrained shear strength of about $>$ 10 kPa, and they normally are deeply oxidized. Furthermore, *Nereites* was not found in sediments affected by indistinct downslope transport from the Philippines (e.g., cores 226, 228, 418, 421, 422; see Fig. 5). These deposits often are burrowed by shallow-tier echinoids that produce the trace *Scolicia*. All of these cores (except 955, 956) mark the eastern boundary of the occurrence of *Nereites*. Nearer to the Philippines, the above factors become more pronounced and *Nereites* is absent.

The 1991 Pinatubo ash represents an excellent marker bed, and it reveals further information about the *Nereites* producers. *Nereites* burrows contain some ash in areas where the ash is thinner than about 2 cm (Fig. 4); therefore, these burrows had been produced recently and their producers were not severely affected by the ash deposition. An average of two ash-filled burrows were found per 450 cm$^2$. If ash thickness exceeds 3 cm, ash was neither observed within the *Nereites* burrows nor was it penetrated by the vertical parts of the burrows. This suggests abandonment of the burrowing activity after ash sedimenta-
FIGURE 4—Nereites in South China Sea sediments and fossil equivalents. (A) horizontal split surface of Permian silt-to-sandstone with *Scalarituba* (= *Nereites*); Oquirrh Formation, Utah. (B)-(F) X-ray radiographs (negatives) showing *Nereites* from the South China Sea. (B) Vertical section. (C)-(F) Horizontal serial sections adjacent to the vertical section shown in (B); C, D, E, and F correspond to 1±2, 2±3, 3±4, and 4±5 cm depth intervals. The visual cross-overs are due to the thickness of the sediment slab that was x-rayed (ca. 1 cm). Burrow segments marked by an "a" indicate 1991 Pinatubo ash within *Nereites* tunnels; Areas marked "h" are reworking halos enriched in coarse grains. All photographs are approximately natural size.
tion. At these sites, the pore water below the ash is oxygen free (Haeckel et al., 2001).

**INTERPRETATION**

The *Nereites* producers appear to be restricted to oxygenated sedimentary environments. The burrows that evidently were produced after 1991 contain ash, and they exclusively occur above the redox boundary and never below. Where the near-surface pore water is anoxic today owing to the deposition of a thick Pinatubo ash in 1991, *Nereites* do not display any sign of continuing activity (i.e., there is no connection to the sediment surface and no ash within the burrows).

The close spatial relationship of the horizontal parts of the *Nereites* burrows to the redox boundary suggests that the animals fed on microbes that are known to occur there in high concentrations (e.g., Köster, 1993). In particular, the nearly constant distance of the *Nereites* level to the redox boundary—dependent of the depth in sediment of the latter—supports this interpretation (Fig. 6). The horizontal parts of the burrow are restricted to a well-defined horizon and, hence, they imply chemotactic guidance of the *Nereites*-producing animals. Nonetheless, the course of *Nereites* is not strictly horizontal. This probably is due to the undulating nature of the upper boundary of the redox zone that results from porosity variation due to earlier bioturbation (e.g., Richardson, 1983) and diffusion within the sediment (e.g., Glud et al., 1994).

The occurrence of some ash within *Nereites* burrows certainly indicates their recent production. The ash infill suggests episodic excursions of the *Nereites* producers to the sediment surface and ingestion of sediment there. *Nereites* producers may take up some additional food, possibly after arrival of organic matter following an upwelling period. So the question arises—can fairly deep burrowing *Nereites* producers recognize the arrival of organic matter on the seafloor? The chemical composition of pore water responds within a few weeks to strongly enhanced organic

**TABLE 1**—Cores containing *Nereites*.

<table>
<thead>
<tr>
<th>Latitude</th>
<th>Longitude</th>
<th>Water depth [m]</th>
<th>Shear strength [kPa]</th>
<th>Organic carbon [% dry weight]</th>
<th>Depth of redox boundary below base of ash [cm]</th>
</tr>
</thead>
<tbody>
<tr>
<td>16°25.03' N</td>
<td>117°20.00' E</td>
<td>4005</td>
<td>0.9–1.7</td>
<td>0.42</td>
<td>8–9</td>
</tr>
<tr>
<td>16°06.06' N</td>
<td>116°59.65' E</td>
<td>4122</td>
<td>0.5–1.4</td>
<td>n.d.</td>
<td>7–9</td>
</tr>
<tr>
<td>15°29.99' N</td>
<td>116°54.98' E</td>
<td>4232</td>
<td>n.d.</td>
<td>0.45</td>
<td>6–7</td>
</tr>
<tr>
<td>15°25.01' N</td>
<td>115°05.01' E</td>
<td>4248</td>
<td>0.8–1.4</td>
<td>n.d.</td>
<td>5±6</td>
</tr>
<tr>
<td>15°06.30' N</td>
<td>115°23.15' E</td>
<td>4262</td>
<td>0.2–1.5</td>
<td>0.52</td>
<td>9–10</td>
</tr>
<tr>
<td>15°03.90' N</td>
<td>115°45.00' E</td>
<td>4220</td>
<td>n.d.</td>
<td>n.d.</td>
<td>8–9</td>
</tr>
<tr>
<td>14°50.14' N</td>
<td>116°54.50' E</td>
<td>4296</td>
<td>n.d.</td>
<td>n.d.</td>
<td>6–7</td>
</tr>
<tr>
<td>14°44.00' N</td>
<td>117°35.99' E</td>
<td>4330</td>
<td>n.d.</td>
<td>n.d.</td>
<td>6–7</td>
</tr>
<tr>
<td>14°39.91' N</td>
<td>118°05.16' E</td>
<td>4251</td>
<td>0.5–0.8</td>
<td>0.46</td>
<td>5–6</td>
</tr>
<tr>
<td>14°39.89' N</td>
<td>118°05.21' E</td>
<td>4254</td>
<td>0.5–0.8</td>
<td>n.d.</td>
<td>5–6</td>
</tr>
<tr>
<td>14°33.0' N</td>
<td>115°08.60' E</td>
<td>4307</td>
<td>n.d.</td>
<td>0.40</td>
<td>8–9</td>
</tr>
<tr>
<td>14°23.01' N</td>
<td>116°03.99' E</td>
<td>4318</td>
<td>0.4–1.4</td>
<td>n.d.</td>
<td>7–8</td>
</tr>
<tr>
<td>14°14.50' N</td>
<td>116°51.34' E</td>
<td>4321</td>
<td>0.3–0.8</td>
<td>n.d.</td>
<td>6–7</td>
</tr>
<tr>
<td>14°10.03' N</td>
<td>113°59.99' E</td>
<td>4323</td>
<td>0.4–1.3</td>
<td>0.57</td>
<td>5–6</td>
</tr>
<tr>
<td>14°03.91' N</td>
<td>117°43.90' E</td>
<td>4152</td>
<td>n.d.</td>
<td>0.60</td>
<td>7–8</td>
</tr>
<tr>
<td>13°50.04' N</td>
<td>116°48.34' E</td>
<td>4326</td>
<td>0.4–1.2</td>
<td>0.40</td>
<td>6–7</td>
</tr>
<tr>
<td>13°40.62' N</td>
<td>116°07.01' E</td>
<td>4345</td>
<td>0.3–1.1</td>
<td>n.d.</td>
<td>7–8</td>
</tr>
<tr>
<td>12°58.27' N</td>
<td>116°09.90' E</td>
<td>4345</td>
<td>0.3–1.4</td>
<td>0.62</td>
<td>9–10</td>
</tr>
<tr>
<td>12°48.01' N</td>
<td>113°33.47' E</td>
<td>4313</td>
<td>0.5–0.8</td>
<td>0.63</td>
<td>5–6</td>
</tr>
</tbody>
</table>
matter accumulation on the sediment surface (Balzer et al., 1987; Soetaert et al., 1996; Gehlen et al., 1997; Haeckel et al., 2001). Such a chemical signal propagating rapidly into the sediment could be directly received by chemically sensitive burrowing animals or indirectly due to the changing position of the redox boundary. Therefore, it is conceivable that the *Nereites* producers, which exploit the sediments just above the redox boundary, could receive chemical signals propagating down from the sediment surface. If so, the excursions of the *Nereites* producers to the surface suggest that they are feeding on the food-rich surface sediment. In the case of the South China Sea, some ash was ingested concurrently.

The ash within the burrows allows an estimation of the population density of the *Nereites*-producing organisms, assuming that the ash infill results from surface feeding following upwelling periods. Calculations based on the studied horizontal sections show that 22 burrows were produced after the Pinatubo eruption during 7 years per m². During this time, high organic matter fluxes were produced after the Pinatubo eruption during 7 years per studied horizontal sections show that 22 burrows were following upwelling periods. Calculations based on the assuming that the ash in®ll results from surface feeding.

ments exhibit a high undrained shear strength of about tive for detritus-feeding animals. Furthermore, these sediments exhibit a high undrained shear strength of about 10 kPa and, therefore, are possibly too stiff for the *Nereites* producers. Sediment grain size is a major control on the distribution of *Nereites* producers. This trace is found in muddy to fine sandy sediments, but not in coarse foraminiferal ooze. In addition, *Nereites* was not observed in areas affected by diffuse downslope transport. There, sediments are buried by *Scolina*, which preferentially occurs in sandy deposits (e.g., Wetzel, 1984; Fu and Werner, 2000). The input of organic matter from land supports intense bioturbation and affects the redox boundary, which renders these areas unsuitable for the chemotactically guided *Nereites* producers.

DISCUSSION

Ecologic factors favoring the production of *Nereites* include soft to soupy, oxygenated sediments that display a well-developed redox boundary near the sediment surface. Water depth affects the amount of organic matter oxidized during settling (e.g., Suess, 1980), but is itself not an important ecologic factor (e.g., Tait, 1971). Conditions for *Nereites* production are more favorable in deep than in shallow water. The *Nereites* producers prefer muds, but they also ingested fine 1991 Pinatubo ash. Coarse foraminiferal oozes, however, were not burrowed by the *Nereites* producers. The critical grain size for the *Nereites* producers appears to be medium sand. Similarly, in the fossil record, *Nereites* is described mainly from distal turbidite settings, where it normally occurs in muds to fine/medium sands (Seilacher, 1962; Uchman, 1995; Wetzel and Uchman, 1998). Such sediments can be penetrated by the organisms ingesting or fluidizing the substrate by body movements (e.g., Schäfer, 1956).

The horizontal parts of *Nereites* suggest a chemotactical guidance of the producers along a fairly sharp redox boundary. From the fossil record chemotaxis is known to affect burrow patterns (e.g., Bromley, 1996), but guidance along a redox boundary has not been reported because it is a temporary feature (e.g., Froelich et al., 1979). Jensen (1992) described the anthozoan *Cerianthus* that inhabits an open burrow system that extends just below the oxic-anoxic boundary in muddy bathyal sediments of the Vöring Plateau (1200–1400 m water depth). He suggested that the animal used microbes (or their metabolic products), which occur abundantly along this geochemical boundary. The polychaete *Paraonis fulgens* displays a change of behavior across the redox boundary in tidal-flat environments. It makes a thigmo-/chemotactically guided spiral to trap diatoms above the redox burrow and a tunnel system below the redox boundary (Röder, 1971).

Chemotactic guidance of trace producers is not unusual and has been reported for many taxa (Bromley, 1996). Therefore, the *Nereites* producers in the South China Sea do not represent an extraordinary behavior for endobenthic organisms. *Nereites* producers appear to be guided by chemical changes in pore water along the upper—still oxygenated—part of the redox boundary.

Consequently, the lower boundary of the *Nereites* tier in the fossil record would reflect the position of the oxygenated interval within the deposits. Habitats characterized by poorly oxygenated pore water and a high benthic food content containing *Nereites* were described, for instance, by Ekdale and Mason (1988) and Wetzel and Uchman (1998) from the fossil record. The food content of the sediment should be sufficient for the *Nereites* producers. Benthic food is too low for the *Nereites* producers if the redox boundary is underlain by previously highly oxidized deposits.

Enhanced accumulation of organic matter on the seafloor resulting from upwelling lowers the flux of oxygen into the sediment (e.g., Gehlen et al., 1997). In response, the *Nereites* producing animals in the oxic zone just above the redox boundary may have moved upward to maintain oxygen supply. Seasonal vertical fluctuations of the position of the redox-boundary may explain the vertical undulation of the *Nereites* burrow (*N. missouriensis*). It is possible that, in sediment not affected by strongly seasonal input of organic matter, the *Nereites* producers strictly follow a horizontal plain (e.g., *N. crassa*, *N. irregularis*, *N. labyrinthisca*).

Surface grazing by subsurface feeders seems to contradict the above findings, but in many instances the behavior of animals is more complex than previously assumed (Kotake, 1989, 1991; Bromley, 1991; Miller, 1998; Miller and Vokes, 1998). Temporary surface feeding by chemical-
ly sensitive deposit feeders may be an underestimated adaptation to utilize an additional food source.

In the fossil record, Nereites belongs to the post-depositional suite of trace fossils colonizing turbidites (e.g., Orr, 1994; Uchman, 1995 and references therein). Seilacher (1962) described post-depositional Nereites that penetrated turbidite sands up to 6 cm thick and exploited the muddy interval below. With respect to the findings in the South China Sea, the post-depositional penetration of a newly deposited turbidite is interpreted as exploration of a buried redox zone that is overlain by a still oxygenated turbidite before the new redox boundary had formed. This is an alternative to adaptation to oxygen-deficient sediments. In fact, a newly deposited turbidite could be oxygenated for some time, as reported by Föllmi and Grimm (1990). The post-depositional, deep-burrowing Nereites producers suggest a slowly re-established redox boundary after turbidite deposition, probably in a highly oxic, organic-poor sedimentary environment.

In the South China Sea sediments the Nereites level marks the upper boundary of the redox zone. Applying this finding to fossil turbidite sequences, the deepest Nereites level would mark the lower boundary of the oxygenated zone. Several factors that control the depth of the redox boundary in modern deep-sea sediments have been discussed. Froelich et al. (1979) invoked the composition of the sediment interval and are absent in anoxic sediments. Furthermore, where the 1991 Pinatubo ash exceeds 3 cm in thickness, Nereites does not show any sign of continuing activity. Such activity is documented at other sites covered by <2 cm ash; where Nereites contain some 1991 Pinatubo ash. The infill of some 1991 Pinatubo ash implies episodic surface feeding activity of Nereites producers, which normally explore the sediment along the redox boundary. In particular, episodes of intensified upwelling and wind mixing enhance the organic matter flux by a factor of 3–4. Such strong episodic input of organic matter probably resulted in a geochemical signal propagating into the sediment and then received by the burrowing Nereites producers. Modelling of oxygen flux into the sediment supports this hypothesis. This organic matter on the seafloor may serve as an additional food source for the Nereites trace-maker. Alternatively, burrowers may have been forced to move closer to the surface due to diminished oxygen contents at their living depth in response to pulsed delivery of organic-rich sediments.

Utilization of sediment along the redox boundary by Nereites producers implies that the Nereites tier in the fossil record, especially in turbidite sequences (flysch), could reflect the long-term position of the paleo-redox boundary. As the depth of the redox boundary in sediment is influenced by many factors, including the sedimentation rate and accumulation rate of organic matter, the depth of the Nereites level potentially could provide a proxy for one or both of these factors.

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