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Effects of a phytodetrital input on nematode communities of the abyssal, equatorial Pacific

by

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ABSTRACT

FACULTY OF SCIENCE
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EFFECTS OF A PHYTODETRITAL INPUT ON NEMATODE COMMUNITIES OF THE ABYSSAL, EQUATORIAL PACIFIC

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Sediment samples were collected at four sites along a latitudinal gradient of phytodetrital deposition from 0 to 9°N at 140°W in the central equatorial Pacific, as part of the US Joint Global Ocean Flux Study, and at a reference site at 23°N, 158°W. Stations at 0-5°N were observed to receive an input of phytodetritus and elevated particulate organic carbon (POC) flux, whereas no phytodetritus was recorded at stations at 9 and 23°N and POC flux was lower. Nematode abundance, biomass, functional group composition and species diversity were quantified. Thes data were used to compare observed patterns of spatial distribution with the predictions of community ecology theory on two scales; small localised patchiness, and latitudinal gradients of change.

Increases in nematode abundance and total biomass were significantly correlated with POC flux (measured into deep-moored sediment traps) along the 140°W transect. Between 0 and 5°N, nematode abundance and biomass in the surface (0-1cm) sediment layer fell at the low end of the range recorded from other previously-studied sites in the NE Atlantic of comparable depth, that are known to receive an input of phytodetritus and elevated POC flux. Total nematode biomass was greatest at 5°N and was highly correlated with 5-month POC flux. It is hypothesised that this reflects the generation times of nematodes responding to POC flux and that previous studies that have failed to record a correlation between nematode biomass and POC flux may be explained by the use of response time-scales derived from cultures of shallow-water nematodes.

Within-habitat (alpha) species diversity was greatest at the equatorial station and decreased with increasing latitude. All alpha diversity indices were significantly, positively correlated with annual POC flux, and quantity of phytodetritus overlying the sediment. Multivariate analysis of the species assemblages indicated that differences in community structure were best explained by annual POC flux.

Comparisons with other previously-studied sites in the NE Atlantic indicates that, at local scales, there is a characteristic faunal assemblage that can be identified as a 'phytodetrital' fauna, at least at the genus level. Regional species diversity in the equatorial Pacific was also correlated with annual POC flux. It was concluded that phytodetritus and/or elevated POC flux enhances the regional nematode species pool.

The equatorial Pacific study also offered a unique opportunity to test theories of the causes of latitudinal gradients of diversity. Latitudinal gradients of POC flux effects in the NE Atlantic are partially confounded by a northwards decline in diversity that has been attributed to recovery from the effects of Quaternary glaciation. The equatorial Pacific has not been influenced by these historical events and nematode assemblages from this location provide compelling evidence that, on a latitudinal scale, gradients in nematode diversity can be attributed to the productivity of the overlying waters.

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dedicated to my parents, Michael and Sheila Brown, for their unfailing support

"A sort of broth ... collects on the bottom of the ocean, derived from the pelagic flora and fauna, from which the lower [animal] types may possibly be able to obtain their sustenance directly"

Alexander Agassiz, 1880

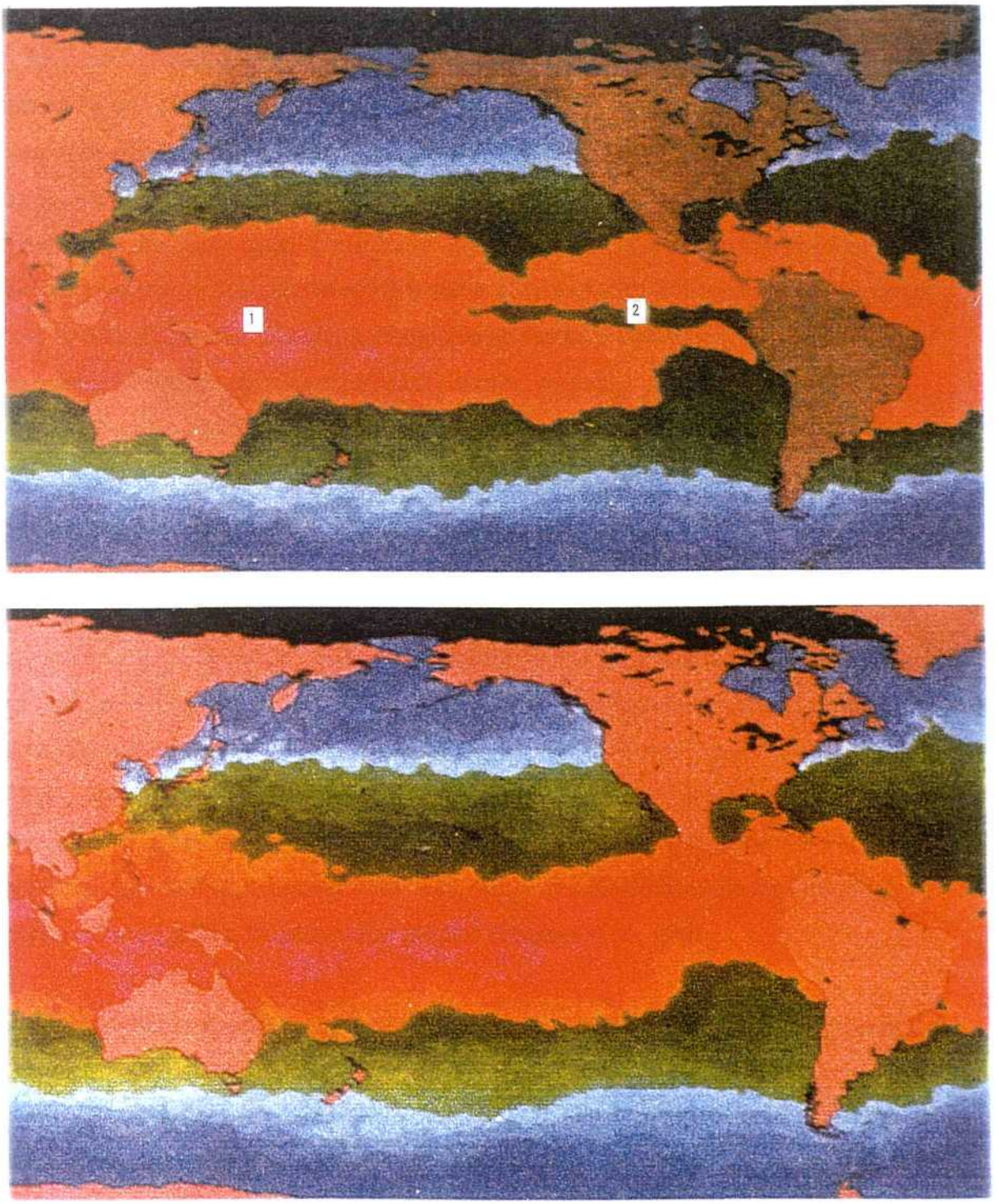
1.1 Surface Current Systems in the Pacific Ocean

The two main gyres of the Pacific Ocean Basin are separated by a complex system of equatorial currents and counter currents. In the Northern Hemisphere, the warm North Equatorial Current forms the longest westward-flowing current in the world's oceans. South of the equator, the South Pacific Gyre dominates water circulation. Surface water flows eastwards as the South Equatorial Current and forms a major gyre with the Australian Boundary Current and the Humboldt Current. The Humboldt Current, a major branch of the Antarctic Circumpolar Current moves northwards along the coast of Chile towards Peru (Mann and Lazier, 1991).

Off the coast of Peru, deflection of the prevailing westerlies by the Andes causes surface water to move offshore to form part of the South Equatorial Current. As a consequence, cold, nutrient-rich water is drawn to the surface (Pernetta, 1994). Off Peru this nutrient-rich, upwelled water stimulates phytoplankton production that makes a significant contribution to global primary production (Chavez and Barber, 1987). Vertical upwelling is constrained to within a degree of the equator and surface divergence of the upwelled water results in a huge tongue of low temperature, high nutrient water. This narrow band straddling the equator extends from the eastern boundary of the Pacific Ocean to the Dateline and is clear in satellite images of sea surface temperature (Figure 1.1). The chemical and biological signatures of this body of water are very distinct when compared with the relatively barren, oligotrophic central gyres of the North and South Pacific, as all of the major nutrients are enhanced i.e. nitrate, nitrite, silicate and phosphate (Murray *et al.*, 1992).

This upwelling feature is subject to temporal instability as a result of the ENSO (El Niño, Southern Oscillation) cycle. Periodically, the major wind patterns of the Southern Pacific weaken leading to changes in the surface currents of the southern gyre and subsequent suppression of the Peruvian upwelling system. The second image in figure 1.1 was taken during such an event and the absence of the cold tongue of water is clearly discernible. As a consequence, major changes in sea level, biological productivity and rainfall patterns

Figure 1.1 Satellite images of the Pacific Ocean during upwelling and El Niño conditions. Blue indicates cool water (0-12°C), green, intermediate temperatures (13-24°C), and yellow, red and purple colours indicate temperatures between 25 and 30°C. The top image taken during January 1994 shows a tongue of cooler water penetrating from the West Coast of Latin America (2). The bottom image was taken during January 1983, at the height of an El Niño event, and shows the warm waters of the western Pacific (1) reaching across the ocean, suppressing the upwelling (taken from Pernetta, 1994).



occur. This change in ocean-atmosphere interactions is termed "*El Niño*" (*the child,* when translated), as it generally occurs in Latin America around Christmas. El Niño is the warm phase of the ENSO cycle and occurs every 7-8 years, lasting for a period of 1-2 years (Pernetta, 1994).

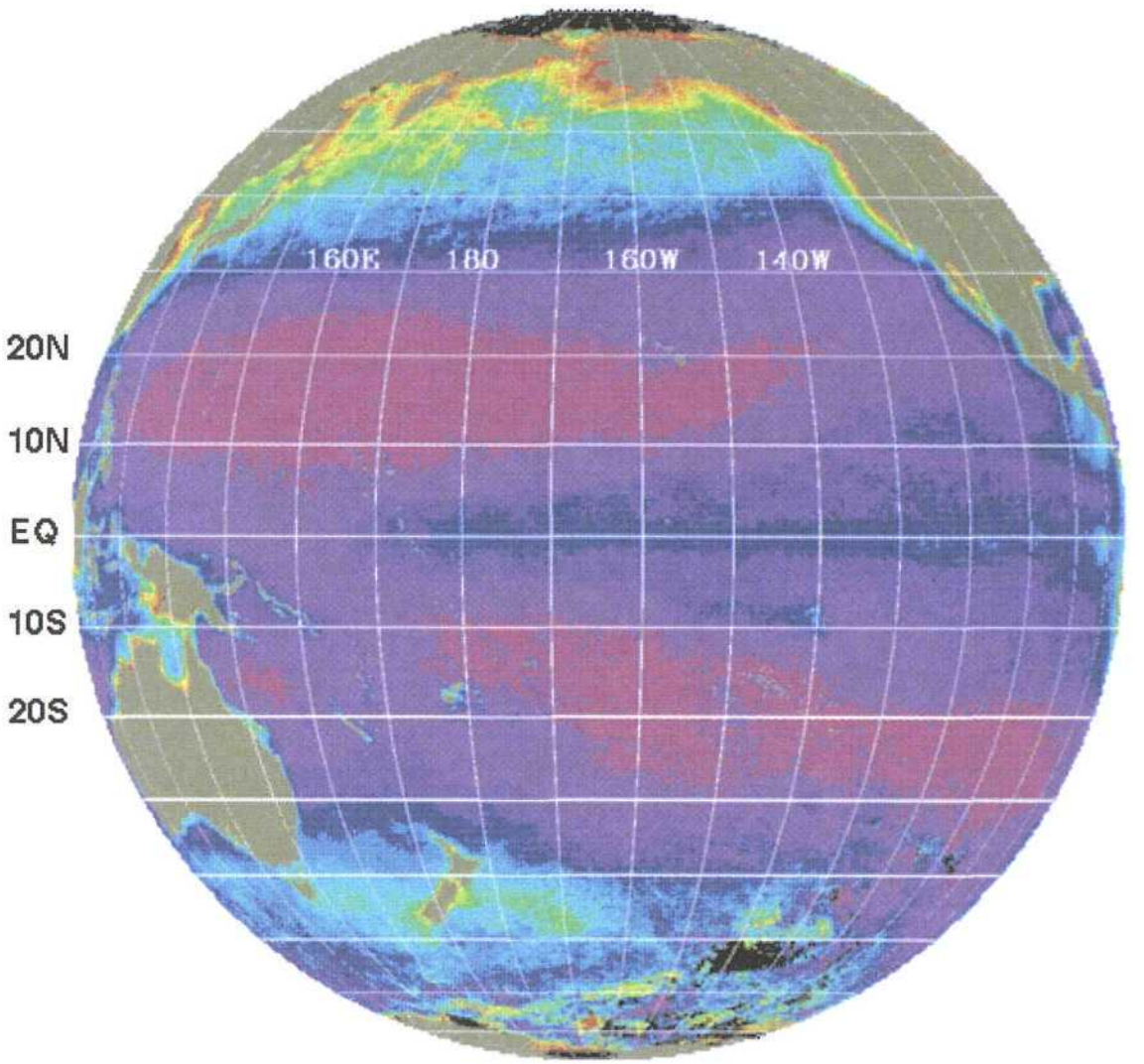
1.2 Productivity in the Surface Waters of the Equatorial Pacific

In the years between El Niño events, biological productivity is enhanced within this narrow tongue of chemically and biologically distinct water along the equator. A composite CZCS (Coastal Zone Colour Scanner) image of the Pacific Ocean (Figure 1.2) shows a region of high phytoplankton pigment concentrations along a narrow band that correlates to this water mass. The band of highest pigment concentrations (0.15mg m^{-3}) is relatively symmetrical about the equator and is approximately 400km in width (Feldman *et al.*, 1992). As a result of its high production and large geographical area, this region of the equatorial Pacific makes a significant contribution to the global flux of carbon and nitrogen. New production (defined as production arising from the utilisation of newly available nitrogen, Dugdale and Goering, 1967) in this region may account for 20-50% of the global ocean value (Chavez and Barber, 1987; Murray *et al.*, 1994).

The flux of carbon within and out of the euphotic zone is thought to be closely related to food-web structure. Malone (1980) suggested that new production is carried out primarily by larger-celled organisms (e.g. chain-forming diatoms) whilst open-ocean productivity is generally regenerated production (defined as production arising from the utilisation of nitrogen recycled within the euphotic zone - mostly ammonia, Dugdale and Goering, 1967) carried out by nano- and pico-plankton. The food web of the equatorial Pacific is dominated by small phytoplankton (Chavez, 1989) with 80-90% of the total chlorophyll being contained within the <2μm size fraction (Murray *et al.*, 1994).

The distribution of size fractions is strongly linked to sinking rates which act to control the structuring of phytoplankton communities (Margalef, 1978). Theoretical predictions and practical observations of sinking rates (Smayda, 1970; Walsby and Reynolds, 1980) have shown that small cells sink more slowly. As the physical processes that enhance the flux

Figure 1.2 A composite Coastal Zone Colour Scanner (CZCS) image for the Pacific Ocean showing a region of enhanced phytoplankton pigment concentrations (0.15mg m^{-3}) along the equator (dark purple). Indicated in pink are the oligotrophic waters of the two oceanic gyres (taken from Feldman *et al.*, 1992).



of nitrate into the euphotic zone also influence the residence time of phytoplankton in the surface layer, the characteristic size structure of the population will be influenced by these physical processes (Malone, 1980). In contrast to coastal upwelling, upwelling in the equatorial Pacific system lacks a shallow sea-floor. In shallow waters, phytoplankton cells are maintained in the euphotic zone by mixing processes, or the establishment of a temporary, shallow thermocline. In the deep ocean, resuspension of larger cells to the surface waters is unlikely so only morphological adaptations, such as possession of flagella or small size, can assist in maintaining position in the surface waters.

In the equatorial Pacific, larger plankton (especially diatoms) are more abundant in upwelling years as a result of the increased turbulence extending the residence time of larger-sized cells in the euphotic zone. The proportion of chlorophyll attributed to diatoms increased from <0.1 to 6% during the 1992 upwelling period (Murray *et al.*, 1994). Additionally, at the northern edge of the upwelled water, a strong convergence zone associated with the front between the cool, upwelled water and warmer waters to the north, was found to concentrate *Rhizosolenia*, a large, chain-forming diatom (Philander, 1989; Pena *et al.*, 1990; Yoder *et al.*, 1994). During an El Niño event, upwelling activity ceases, there is a corresponding drop in turbulence, and abundance of the larger phytoplankton decreases.

1.3 The US Joint Global Ocean Flux Study in the Equatorial Pacific

The equatorial Pacific process study was conducted as part of the multidisciplinary US Joint Global Ocean Flux Study (JGOFS) during 1992. The central and eastern equatorial Pacific Ocean is the largest oceanic source of carbon dioxide to the atmosphere (about 0.9 gigatons of carbon per year), i.e. it is a site of major carbon fluxes. The purpose of the study was to determine the nature of these fluxes and related elements, and the processes controlling the fluxes between the atmosphere, surface ocean and deep ocean. These fluxes vary inter-annually with the ENSO cycle and the study was fortuitously timed to coincide with the extreme conditions of a major El Niño event, thus providing a unique set of surface-water chemistry and biology samples for El Niño conditions.

In addition, pelagic studies addressed the mechanisms that make the equatorial Pacific a HNLC (high nutrient, low chlorophyll) region and the factors that control carbon dioxide gas exchange, and new and export production. Benthic studies attempted to determine the fate of carbon in the deep sea and the preservation of the primary productivity signal in buried sediments. It is the fate of carbon originating in the surface waters which forms the basis of this study.

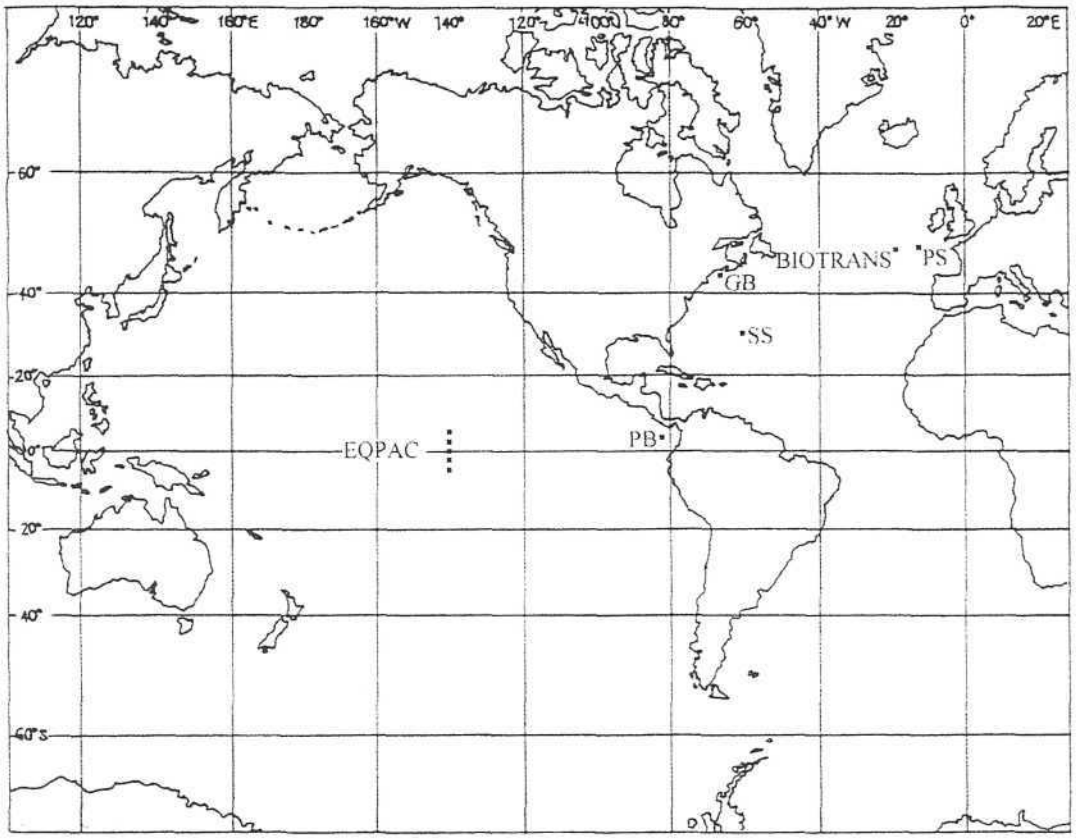
1.4 Phytodetritus and its Role in the Deep Sea

For many years, it was thought that organic carbon flux exported from the euphotic zone reached the seafloor as a slow and sparse rain of particulate organic matter (e.g. Riley *et al.,* 1964), known as *marine snow*. More recently, evidence from sediment traps (Deuser and Ross, 1980; Honjo, 1982; Smetacek, 1985) and *in situ* photographs of the sea floor (Billett *et al.*, 1983; Rice *et al.*, 1986) indicated that significant, rapid, vertical transport of phytoplankton from the upper ocean to the deep sea must occur. In temperate, polar and coastal seas this rapidly sinking phytoplankton is often dominated by diatoms, which arrive at the seafloor relatively intact (Billett *et al.*, 1983; Takahashi, 1986; Thiel *et al.*, 1988/89).

Large amounts of this *phytodetritus* were first observed on the seafloor of the Porcupine Seabight in the Northeast Atlantic at depths between 1,370 - 4,100m (Billett *et al.*, 1983). Further sampling in this area indicated that these deposits occur as a seasonal pulse during May to August that coincides with surface phytoplankton blooms (Lampitt, 1985; Rice *et al.*, 1986). Subsequent studies have found evidence of phytodetrital material in the Sargasso Sea (Deuser and Ross, 1980), the Panama Basin (Honjo, 1982), the Georges Bank, NW Atlantic (Hecker, 1990) and in a mid-oceanic region of the Northeast Atlantic - the BIOTRANS site (Thiel *et al.*, 1988/89) (Figure 1.3).

Recently, studies in the central equatorial Pacific have also discovered abyssal accumulations of phytodetritus (Smith *et al.*, 1996) over a broad latitudinal distribution (>10° latitude) (Figure 1.3 and Figure 1.4). Contrary to those sites in temperate waters, however, phytodetrital input appears to be quasi-continuous, as a consequence of the

Figure 1.3 Map showing locations of areas where phytodetritus has been observed overlying deep-sea sediments. PS = Porcupine Seabight, GB = Georges Bank, SS = Sargasso Sea, PB = Panama Basin and EQPAC = 5°S to 5°N equatorial Pacific stations. See text for references.



coastal upwelling, which enhances surface productivity year-round. Accumulations on the seafloor correlate well to the pattern of surface primary productivity (Figure 1.4) suggesting a causal effect. Clearly shown in the diagram is the pulse of productivity that occurs in the convergence zone at about 2°N.

In addition to direct observations of deposited phytodetritus in the equatorial Pacific, evidence was also found in the geological record. Vast, Neogene, laminated deposits were discovered in the eastern equatorial Pacific Ocean (Kemp and Baldauf, 1993). It was surprising that such deposits were found at all, as bioturbation by the benthic community would be expected to disrupt laminations like these. It would seem that deposition occurred so rapidly that the benthos was overwhelmed and unable to penetrate the mats.

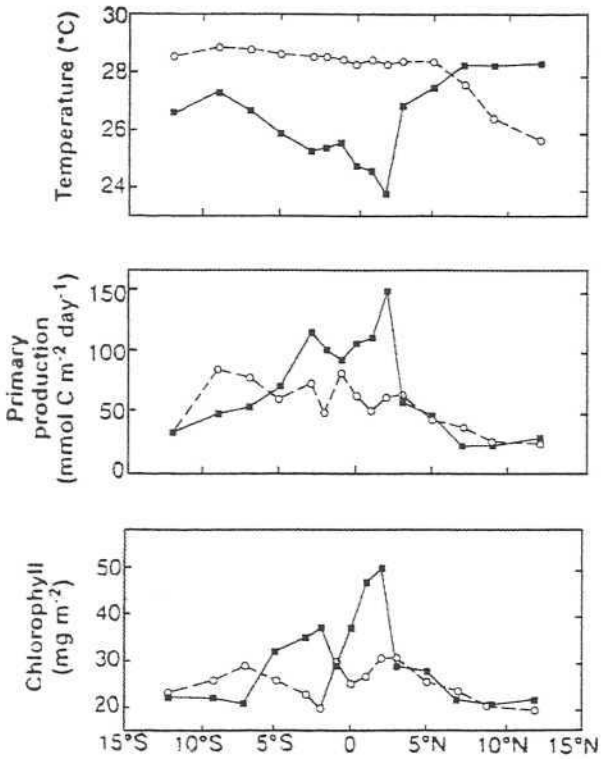
In the Porcupine Seabight and on the Northeast Atlantic slope, phytodetritus can occur in uniform greenish carpets up to 1cm thick in places (Billett *et al.*, 1983; Lampitt, 1985). At the BIOTRANS site (NE Atlantic), cover is very heterogeneous and subject to resuspension (Thiel *et al.*, 1988/89). Consequently the detrital material is often apparent as patchy deposits (Billett *et al.*, 1983; Rice *et al.*, 1986; Thiel *et al.*, 1988/89) rather than sheets, as in the Porcupine Seabight.

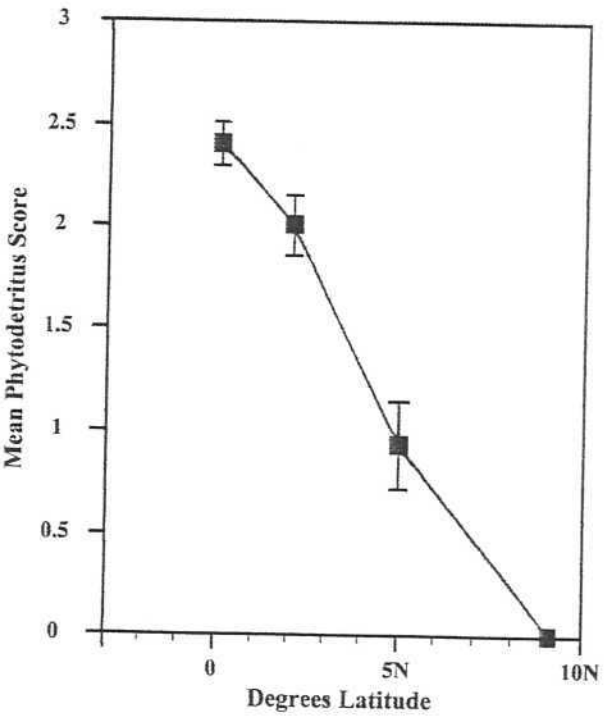
Examination of the composition of this detrital material finds it to be in good agreement with the phytoplankton communities of the overlying water. This close similarity suggests rapid transport of the detrital material. Additionally, chemical analyses indicate the presence of measurable quantities of chlorophyll *a* (Billett *et al.*, 1983; Rice *et al.*, 1986; Thiel *et al.*, 1988/89) and excess ^{234}Thorium (^{234}Th) (Stephens *et al.*, 1997). As these two tracers have degradation time-scales of less than one hundred days (Stephens *et al.*, 1997), their presence implies that the phytodetritus reaches the sediment within this time period. The results of Billett *et al.* (1983) suggest a sinking rate of 100-150 m day^{-1} in the Porcupine Seabight, which compares well with that of Pacific diatom populations, estimated by Takahashi (1986) at 175m day^{-1}.

This rapid removal of particulate organic material from the surface waters offers a significant route for net downwards flux of carbon and nitrogen. Within the BIOTRANS area, estimates based upon the quantity of phytodetritus on the seafloor suggest that up to

Figure 1.4 Sea surface data (a) and seafloor data (b) from a meridional transect from 12°S to 12°N along 140°W. In (a) O indicates data collected during an El Niño event and ■ = data collected during a period of upwelling (modified from Murray *et al.*, 1994). In (b) the mean phytodetritus score was based upon the visual inspection of multiple cores collected along the transect as follows: 0 = no visible flocculent material on core top, 1 = small amount (0-10% cover) of greenish material on top, 2 = substantial amount (10-90% cover) of greenish flocculent material, 3 = essentially complete cover of sediment-water interface (modified from Smith *et al.*, 1996).

(a) (b)





3% of surface water-spring primary production reaches the seabed at 4,500m (Thiel *et al.*, 1988/89). The phytodetrital standing crop in the equatorial Pacific was as high as 2.6mmol C_{org} m^{-2} (Smith *et al.*, 1996) and 5.8-32 mmol C_{org} m^{-2} at the BIOTRANS site (Thiel *et al.*, 1988/89).

Although the percentage of surface-water primary production reaching the deep-sea bed is small and its organic carbon content surprisingly low (Rice *et al.*, 1986), its role in the benthic ecosystem is of crucial importance. Rapid disappearance of the detritus following sedimentation (Rice *et al.*, 1986) suggests fast biological breakdown and incorporation into the sediment. Consequently, the input of carbon in the form of phytodetrital material would be expected to have a significant impact on the benthic communities of the deep sea.

Rice *et al.* (1986) studied cores from the Porcupine Seabight that had an overlying layer of phytodetritus, and compared them with cores that did not. Although there were no significant differences in bacterial biomass estimates or total counts, significantly higher frequencies of dividing cells and larger mean cell volume suggested that microbial activity was greater within and immediately below detrital aggregates. Similarly, Smith *et al.* (1996) noted a significant increase in the uptake of radio-labelled glutamate in samples of phytodetrital collected from the equatorial Pacific, which they attributed to greater microbial activity. At the BIOTRANS site in the NE Atlantic, bacteria were significantly more abundant in sediments collected in July-August 1986 than in sediments collected before the phytodetritus depositional event in May 1985 (Thiel *et al.*, 1988/89). The presence of bacteria and their transformation of the detrital material may enhance the role of phytodetritus in nutrition of the benthos.

Turley and Lochte (1990) demonstrated that, at the abyssal BIOTRANS site, elevated microbial activity could be attributed, at least in part, to benthic components of the microbial community. Sterilised, artificial phytodetritus was incubated with sediment top water and it was discovered that rate of bacterial decomposition was significantly faster at 450atm, indicating that some components of the microbial community were barophilic.

Some Foraminifera also respond directly to phytodetritus. In the BIOTRANS material, detritial aggregates collected during July-August 1986 were dominated by three species which were much less abundant both in the sediment communities, and also in samples collected before deposition of phytodetritus (Thiel *et al.*, 1988/89). The same species were also dominant in samples of phytodetrital material collected from the Porcupine Abyssal Plain (Gooday and Lambshead, 1989). There are several lines of evidence to indicate that these foraminiferans feed on phytodetritus (Gooday and Turley, 1990): firstly, the green coloration of their protoplasm is thought to be derived from chlorophytes found in the detrital material; secondly, all three species display bright orange autofluorescence that is characteristic of cyanobacteria colonising the phytodetritus; and thirdly, from direct observations of feeding activity in incubation experiments conducted *in situ* (Turley *et al.*,1993). Gooday and Turley (1990) hypothesised that benthic foraminiferans rapidly colonise deposited phytodetrital material, subsequently reproducing rapidly to build up large populations dominated by a small number of colonising species.

It was suggested more than one hundred years ago that some abyssal echinoderms may feed on phytoplankton remains in the deep sea (Castracane degli Antelminelli, 1886 in Gooday and Turley, 1990). Analyses of gut contents from four holothurian species discovered the presence of chlorophyll pigments and their degradation products, confirming photographic evidence of browsing activity on phytodetritus by one species (Billett *et al.*, 1988). Bottom photographs have also indicated that other echinoderms, notably an ophiuroid and an echinoid, are attracted to patches of phytodetritus (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986; Grassle and Morse-Porteous, 1987; Billett *et al.*, 1988). Tyler (1988) and Tyler and Gage (1984) proposed that a direct link exists between the deposition of phytodetritus and seasonal patterns of reproduction in some deep-sea echinoderms and other taxa including isopods, bivalves, brachiopods, scaphopods, actinians, decapods and macrurid fish (Harrison, 1988; Tyler, 1988). The increase in food availability is thought to either ensure survival of larvae or meet the energy demands made by the vitellogenesis process, which is observed during summer and autumn in some invertebrate species (Tyler *et al.*, 1982). Utilisation of phytodetritus for somatic growth has also been invoked to explain the occurrence of growth rings in shells of bivalves and brachipods, in calcareous skeletal plates in echinoderms, and in the otoliths of fish collected in the deep sea (Tyler, 1988). In shallow waters, growth bands are .

usually attributed to variations in growth rate as a result of temperature-induced increases in metabolic rate or food supply, but temperatures are constantly low in the deep sea, suggesting that seasonality in the supply of organic material may be responsible.

There is a considerable evidence documenting a response by a wide variety of taxa to the input of phytodetritus in the deep sea. It seems reasonable, therefore, to predict that phytodetritus will also significantly impact the nematode communities of the abyssal equatorial Pacific.

1.5 Meiobenthology

Mare (1942) originally coined the term 'meiobenthos' from the Greek '*meion*' meaning smaller. It described an assemblage of organisms that was distinct from the macrofauna and microfauna and was separated on an empirical basis, i.e. all animals passing a 500μm sieve mesh but retained on a 45-63μm mesh. Within the meiofauna, a further division can be made into what McIntyre (1969) termed the permanent and temporary meiofauna. The temporary meiofauna comprise the larval, generally settlement, forms of adult macrofaunal species which quickly grow out of the size range of meiofauna. The permanent meiofauna include groups such as the Nematoda, Harpacticoida, Gastrotricha, Kinorhyncha, Tardigrada, Ostracoda, Gnastholmulida, Turbellaria, Archiannelida and a few specialised members of other groups generally considered to belong to the macrofauna. In fact, all of the known metazoan groups are represented, including some unusual forms known exclusively from marine sediments. All free-living nematodes are considered to be members of the meiobenthos or meiofauna and are probably the most abundant metazoan organisms in the biosphere.

Nematodes (used here, this term will refer to free-living, marine forms only) make up the most important and abundant metazoan group in marine (littoral, estuarine, coastal and oceanic) sediments, extending from the high-water mark to the deepest ocean trenches (Nicholas, 1975). They form the most abundant taxon within the meiofauna, accounting for up to 90-95% of individuals. They regularly reach densities of millions per square metre, especially in muddy estuarine sediments. Indeed, Warwick and Price (1979)

recorded an astonishing 23 million per square metre in the Lynher estuary (UK). Even in the deep sea, numbers may reach 0.1 million per square metre (Lambshead, 1993).

In addition, nematodes exhibit an extremely high species diversity. The number of species present in any one habitat is usually an order of magnitude higher than for any other taxon (Platt and Warwick, 1980). About 4000 species of nematode have been described so far, belonging to some 450 genera. Across all biotopes, it has recently been estimated that up to 100 million species of marine nematodes may exist (Lambshead, 1993) and, consequently, small samples may be used for ecological research, as compared with macrofauna, to obtain statistically robust data.

Despite their very small size, nematodes make a significant contribution to the meiofaunal biomass of marine sediments, some 50-90% (Gray and Rieger, 1971). They have a high metabolic rate and relatively short life cycles (days/months) which means production rates are also high (Gerlach, 1971; Warwick *et al.*, 1979).

Nematodes are also, theoretically, ideal candidates for use as indicators in biological monitoring of environmental pollution (Tietjen and Lee, 1977; Platt, 1984). Many species exhibit short generation times (time from egg to egg in successive generations) with generally conservative reproductive strategies and lack a dispersal phase in their life histories. This means that nematode populations can respond rapidly to changes in environmental conditions. These changes are readily discernible and, theoretically, easily related to external variables. The variables may not necessarily be restricted to environmental contaminants, but may also include natural perturbations examined in ecological studies.

Prior to 1960, no information was available on the abundance, diversity or standing crop of meiofauna in the deep sea. The deep-sea is the world's largest biotope and, as yet, remains relatively unexplored. This is primarily due to the increased difficulty, and hence expense, of working in this particular marine environment, but is also due, in part, to sampling techniques used in early deep-sea expeditions. Right up to the 1960's, the deep-sea environment was perceived as a virtual desert where little could survive, due to the harsh, inhospitable conditions of complete darkness, low temperature and immense

pressure. Early collectors used large-meshed collecting nets that caught only the large, scarce megafauna and because the majority of deep-sea organisms are so small, they slipped through the nets unnoticed.

Hessler and Sanders were the first to utilise fine-meshed, epibenthic sleds that scraped off the top centimetres of sediment, in a series of deep-sea ecological research programmes in the 1960's. Suddenly an astonishing variety of small animals was revealed. However, even after the introduction of box corers, which bite out a measured chunk of the sediments and return them undisturbed to the surface, the favoured mesh size employed for sieving such samples was 500 μm and hence most of the meiofauna was lost. Using fine-meshed sieves, Wieser (1960) was the first to compile data on meiofauna and postulated a decrease in meiofaunal abundance with depth, in parallel to the already-known decrease in macrofaunal abundance. From then on, some effort has been made to obtain reliable quantitative data on the abundance of meiofauna in general, and nematodes in particular. This was aided in part by the introduction of a framed multiple-corer for careful sediment penetration. A pressure wave in front of a grab or box corer often stirs up the top few millimetres of detritus that is particularly rich in meiofauna. This sampling disturbance was also responsible, together with low-resolution sieve meshes, for the late recognition of meiofaunal abundance and composition in the deep sea.

Even with the use of sophisticated instrumentation such as the multiple-corer and the application of newly-developed analytical methods (e.g. measurement of chloroplastic pigments, adenosine nucleotide content and electron transport system ability), our view of deep-sea meiofauna remains rather fragmented and restricted to those areas where interested meiofaunal researchers tend to be based. It has been estimated that less than 21.5 m^2 of the deep-sea floor from all the world's oceans has been sampled for meiofauna (Vincx, pers. comm.) compared with about 2km^2 for macrofauna (Paterson, 1993) and yet about half of the Earth's surface is deep sea, with more than one kilometre of overlying water.

1.6 Objectives

There is considerable current interest in the pelagic and sedimentary processes at the equatorial Pacific convergence zones, but there is very limited literature describing the benthic fauna or the community ecology of equatorial Pacific (EqPac) nematodes. Although some studies have considered the meiofauna of the abyssal Pacific ocean, with the exception of the studies of Shirayama (1983; 1984a; 1984b) in the western Pacific, nematodes have generally been included as part of the meiofauna, without even low-level taxonomic distinction. This research study will address this lack of information by examining a suite of meiofaunal samples and making an accurate taxonomic assessment of the nematode species assemblages within them. In addition, the spatial distribution of nematode communities will be assessed. It is proposed to test these spatial patterns against the predictions of community ecology theory on two scales, small localised patchiness and latitudinal gradients of change.

The objectives of the current study were fourfold:

1. To examine the impact of phytodetritus on nematode abundance and biomass, including body size

2. To assess changes in community trophic structure as revealed by feeding type and tail shape

3. To determine changes in nematode species diversity within and between habitats

4. To compare the effects of phytodetritus in the equatorial Pacific with previous studies in the NE Atlantic to determine whether effects reflect ecological or historical processes.

1.7 Hypotheses

- Elevated particulate organic carbon (POC) flux is not correlated with a significant increase in nematode abundance or biomass in the abyssal, equatorial Pacific

Chapter 4

- Bioturbation effects by larger organisms are not correlated with the vertical distribution of nematode abundance or biomass

Chapter 4

- Elevated POC flux is not correlated with an increase in mean body size in EqPac nematodes

Chapter 4

- Elevated POC flux and its associated environmental variables (i.e. bacterial content, sediment type) are not correlated with the trophic structure of EqPac nematode communities

Chapter 5

- Bioturbation effects by larger organisms are not correlated with the vertical structure of nematode functional groups

Chapter 5

- Phytodetritus and/or elevated POC flux are not correlated with nematode α (within-habitat) or β (between-habitat) diversity

Chapter 6

- Phytodetritus and/or elevated POC flux are not correlated with changes in species-level community structure

Chapter 6

- The occurrence of phytodetritus in deep-sea ecosystems is not correlated with high regional diversity

Chapter 7

2.1 Community Ecology Theory

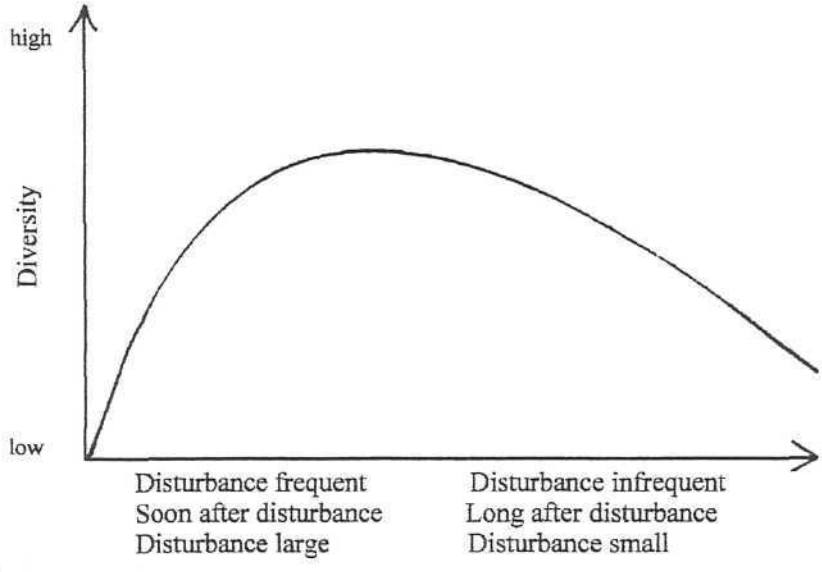
For much of this century, most researchers in ecology believed in the *Equilibrium Paradigm* as the theoretical basis for community ecology. The Equilibrium Paradigm predicts that, under normal conditions, the species in a community are in a state of competitive equilibrium. This balanced community has a higher diversity than disturbed communities and any shift away from equilibrium reduces diversity. The *Stability-Time Hypothesis* of Sanders (1968) demonstrates the basic principles of equilibrium ecology. In his classic, comparative study of marine benthic diversity, Sanders suggested that physical stability in the deep-ocean environment has permitted extreme, adaptational specialisation to develop on an evolutionary time-scale to minimise competitive interactions between potentially competing species. In contrast, in environments where physical conditions are less predictable, physiological stress is a precursor to tolerance of a wide variety of physical conditions, and hence precludes the high diversity resulting from evolutionary divergence into a wide range of separate niches. Sanders used examples from soft bottom communities and demonstrated that shelf-faunas of polychaetes and bivalves were less diverse than those of the deep sea.

Within the last twenty years, however, a number of examples from field observations have been recorded that can not be explained by equilibrium theory. As a consequence, belief in the Equilibrium Paradigm has dwindled as a suitable explanation for patterns of species diversity. In its place a new paradigm has been conceived in which communities are thought to exist in a state of *non-equilibrium* and the level of predictability in a community is less certain.

An important paper in establishing an alternative theory to the equilibrium paradigm was a study by Connell (1978), in which his alternative theory was tested and compared with the predictions of a number of equilibrium and non-equilibrium hypotheses, using data from two highly diverse environments. He called his theory *the Intermediate Disturbance Hypothesis* and attempted to answer the question – how is high species diversity maintained in tropical rainforests and coral reefs?

Connell (1978; 1979) identified disturbance as being the key process, acting to create space by killing or removing organisms. It was clear to him that the frequency of natural disturbance and the rate of environmental change are often much faster than the rates of recovery from such perturbations. Connell argued that competitive exclusion was rarely achieved in natural populations as other forces set back, deflect or slow the process of return to equilibrium (see also Wiens, 1984). This maintains local assemblages in a non-equilibrium state. Connell went on to suggest that at some optimum point, some *intermediate* level of disturbance, a community will reach its maximum diversity (Figure 2.1).

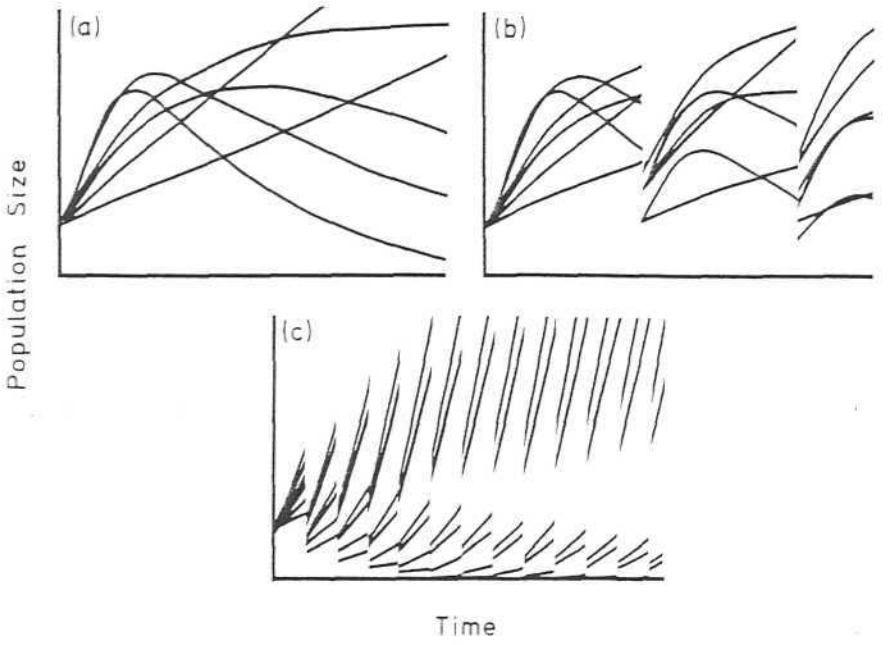
Figure 2.1 The Intermediate Disturbance Hypothesis (from Connell, 1978).



A year after Connell's groundbreaking theory, Huston (1979) published a paper that also examined the effects of disturbance on populations. Huston's approach does not consider comparisons of competitive ability but instead the rates at which different competitive abilities are expressed – the *rate of competitive displacement*. This is actually the rate of approach to competitive equilibrium, and hence a reduced rate of competitive displacement allows a prolonged period of coexistence, thus maintaining diversity. Huston's model was based upon computer simulations that examined the dynamic, non-equilibrium behaviour of the classic Lotka-Volterra competition equations (Figure 2.2). As noted by Connell (1978; 1979) and Dayton (1972), intermediate levels of periodic population reduction (disturbance)

were best at slowing the rate of competitive displacement, thus maintaining diversity. Huston's model is a simple yet intuitive mechanism by which quantitative environmental differences may affect community structure. Diversity is maintained by the influence of the environment on the net outcome of the interactions of competing species.

Figure 2.2 Effects of frequency of population reductions on maintenance of diversity, based upon computer simulations of Lotka-Volterra competition equations for six species. (a) no reduction; diversity is reduced as the system approaches competitive equilibrium. (b) periodic reductions; diversity is maintained for a longer time than in (a). (c) high frequency of reductions; diversity is reduced as low density populations are unable to recover (from Huston, 1994).



To conclude, it is now believed that non-equilibrium dynamics rather than equilibrium processes may best describe many natural systems. The term community is often interchanged with assemblage and implies no higher predictability. Disturbance has been highlighted as an important ecological process and this is probably best defined as:

> *"a discrete punctuated killing or displacement that creates an opportunity for new individuals to become established."* (Sousa, 1984)

It is also important to consider what spatial and temporal scales are being studied. It would appear to be true that over short time-periods, or on localised scales, disturbance, be it physical or biological, is important for determining the diversity of a particular assemblage. However, on longer evolutionary timescales, or over much larger geographical areas, equilibrium concepts, such as competition and niche specialisation, may be of greater importance. Sousa (1979) noted evidence of a global equilibrium/local non-equilibrium phenomenon in species composition of intertidal boulder-field communities.

Wiens (1984) suggested that the two paradigms ought not to be considered mutually exclusive and that instead a gradient of states exists, ranging from non-equilibrium to equilibrium extremes. At the poles of this spectrum, certain features of the community can be described (Table 2.1). It was proposed that the way forward for community ecology research is to determine where, on this spectrum, natural systems could be placed.

2.2 Disturbance and Patch Dynamics in Marine Ecosystems

In both Connell's and Huston's models, disturbance is perceived as creating patches devoid of organisms that are ripe for colonisation. It was this part of these theories that gave the Non-Equilibrium Paradigm the advantage over equilibrium theories. Patchiness was deemed to be a normal element of any environment (see reviews in Pickett and White, 1985) at a wide range of spatial and temporal scales and intensities. For example, at one extreme the communities associated with hydrothermal vents are

Table 2.1 Attributes of community structuring or dynamics at the poles of the non-equilibrium/equilibrium spectrum (from Wiens, 1984).

Non-equilibrium	**Equilibrium**
Biotic decoupling	Biotic coupling
Species independence in response to environmental fluctuations	Competition
Habitats undersaturated and species under-represented	Saturated habitats
Populations strongly affected by abiotic limitation	Populations suffer resource limitation
Population dynamics fuelled by density-independent effects	Population dynamics fuelled by density-dependent effects
Individuals are opportunists	Individuals are specialists
Stochastic environmental effects are important	Few stochastic effects
Communities are loosely structured and lack clear patterns	Communities are tightly structured with predictable patterns

qualitatively distinct from those on the surrounding seafloor with few species in common (Tunnicliffe, 1992). These faunal-rich zones may cover areas some tens of metres in diameter. At the other end of the spatial-temporal-intensity spectrum, are dense aggregations of the brittlestar, *Ophiophthalmus normani,* reported from the Santa Catalina Basin (Smith and Hamilton, 1983). These aggregations are thought to be linked to breeding and are small (measured in centimetres), very ephemeral (lasting minutes to hours) and involve the dominant organism in the general area. Between these two extremes lies a wide range of patch types (Figure 2.3).

Patchiness can be defined as:

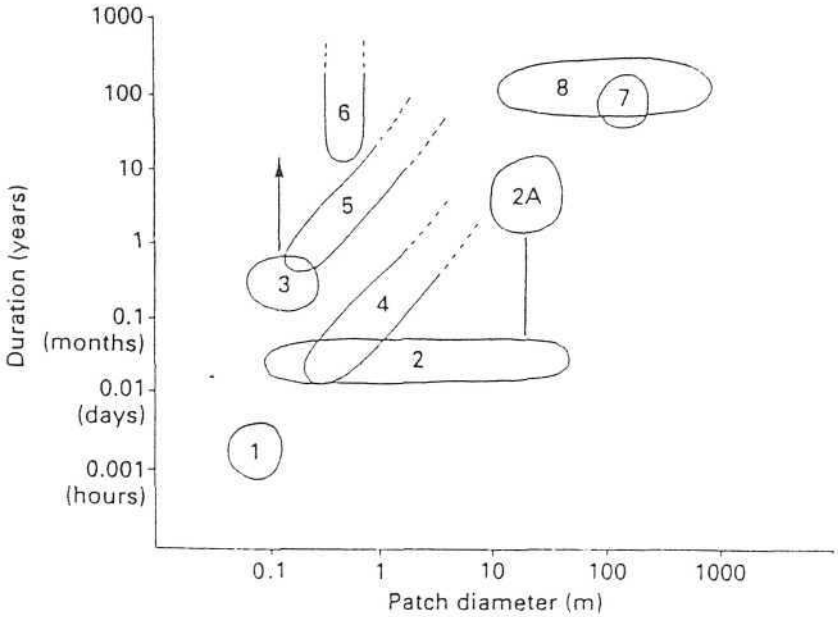
> *"distributions of organisms in space which deviate from randomness in the direction of aggregation rather than regularity"* (Rice and Lambshead, 1994)

Generally, when considering benthic fauna, patchiness has been considered by researchers only in terms of horizontal spatial variation and not any non-random distributions of organisms that may occur vertically within the sediments. Additionally, only spatial structure *within* communities or populations is considered. Knowledge of patchiness can help to specify the reliability and precision of population density estimates. Furthermore, the underlying causes of patchiness can provide information about biotic and abiotic interactions on the deep-sea floor and may help to explain the high diversity found there.

The observation that habitats are made up of a mosaic of patches, each at a different stage of recovery from a disturbance event, was one made before the development of the Intermediate Disturbance Hypothesis. Grassle and Sanders (1973) considered patches as being important for maintaining species diversity over ecological timescales, and Johnson (1970) considered intertidal fauna to exist as a mosaic of patches.

The deep sea is not the monotonous and structureless habitat it was once perceived to be. Instead, even the most dynamic of soft-bottomed environments, such as the HEBBLE (High Energy Benthic Boundary Layer Experiment) site, are subject to microtopographical features such as feeding mounds and pits, sand waves and ripples, and tubes and burrows (Aller and Aller, 1986). Sampling indicates contiguous distributions of

Figure 2.3 Spatio-temporal scales of a range of deep-sea faunal aggregations (from Rice and Lambshead, 1994).



No.	Reason	Example	Reference
1	social/breeding aggregations	*Ophiophthalmus normani* (Ophiuroid)	(Smith and Hamilton, 198
2	slow-moving deposit feeders/'herds' feeding on generally-distributed resources	*Echinus affinis* (echinoid)/ *Scotoplanes* (holothurian)	(Grassle *et al*, 1975; Smith and Hamilton, 1983)
3	feeding on patchy resources	nematodes, foraminifera	(Rice and Lambshead, 1994)
4	scavenging on carcasses (at upper end of scale - specialised vent fauna on whale remains)	Epibenthic scavengers	(Smith, 1985b; Smith, 1986; Smith and Brumsickle, 1989)
5	aggregations on plant remains	benthic infauna	(Grassle and Morse-Porteous, 1987)
6	macrofaunal aggregations on hexactinellid sponge populations	benthic infauna	(Rice and Lambshead, 1994)
7	immobile suspension feeders	Pheronema carpenteri (sponge)	Rice et al, 1990
8	Vent and seep populations		(Tunnicliffe, 1992)

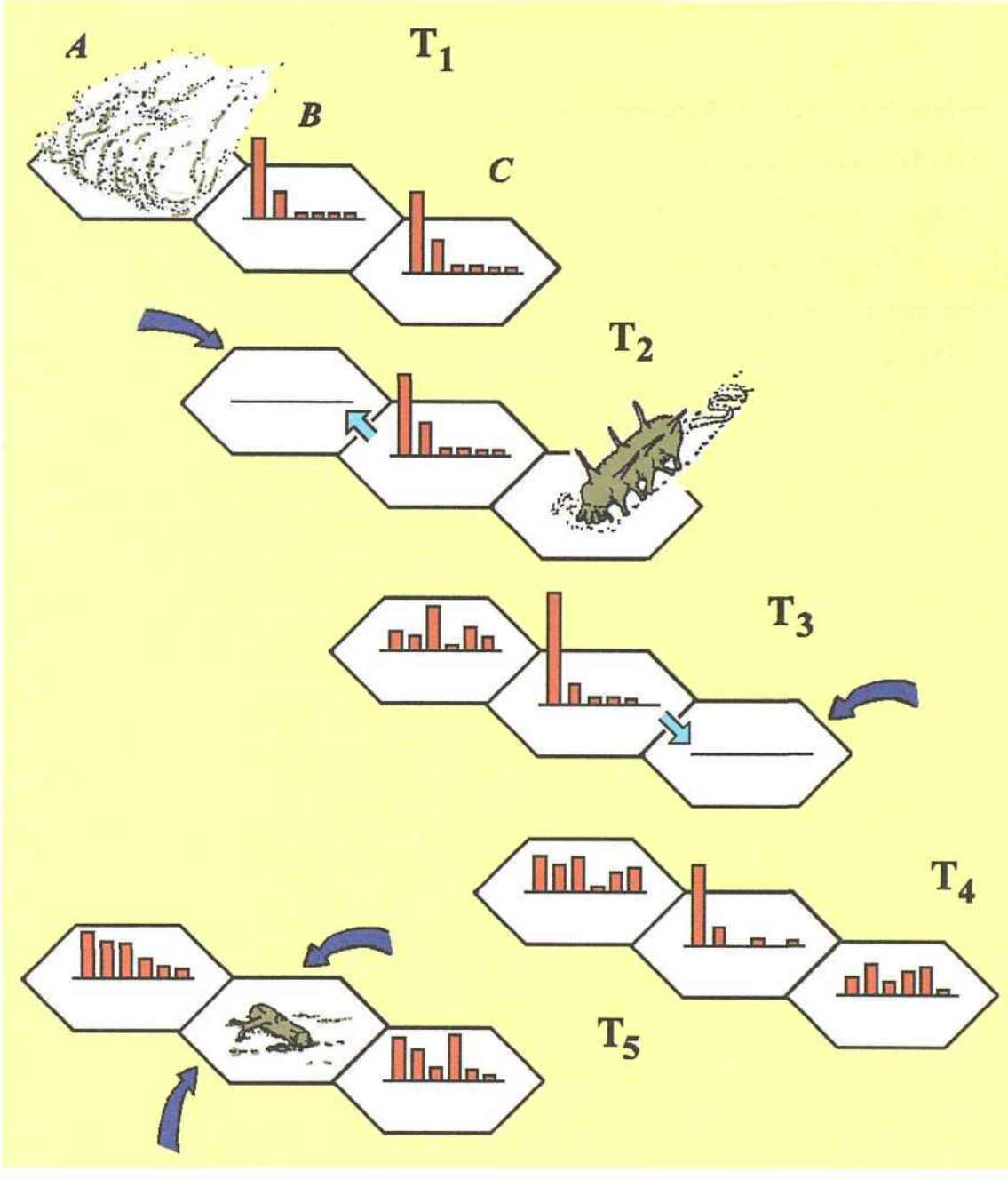
infauna suggesting that aggregations occur. In soft sediments, patches are not as clearly delineated as, say, a tree fall in a forest, but even in many sheltered habitats, distinct patches can be observed. In the deep sea in particular, very low sedimentation rates mean that biologically-generated habitat heterogeneity may persist for longer than in shallow-water or more energetic environments.

Currently, two main theories have been proposed to explain patterns of diversity as a consequence of this habitat heterogeneity. The first of these is the *Spatio-temporal Mosaic* or *Contemporaneous Disequilibrium Theory* (Richerson *et al.*, 1970; Thistle, 1981; Rex, 1983; Grassle and Morse-Porteous, 1987). According to this theory, patches are created by disturbance events and a habitat consists of a mosaic of such patches, each at a different stage of recovery following recolonisation. The species composition varies with time from disturbance, i.e. soon after recolonisation there is little competition for resources and diversity increases as more species colonise. Eventually, if disturbance does not recur, then some species will become dominant at the expense of diversity. At some intermediate disturbance level (i.e. of frequency and intensity), the diversity of a region will be high, as many patches are not dominated (Figure 2.4). This is very similar to the Intermediate Disturbance Hypothesis of Connell (1978) and the equilibrium spatial variation model of Levin (1974).

Paterson (1993) postulated the sequence of events thought to occur within a number of patches experiencing disturbance events at different times. According to his diagram (Figure 2.4): at time period T_1, patch A experiences a disturbance in the form of an eroding current. The other patches meanwhile are demonstrating similar abundance patterns. At T_2, patch A is recolonised by immigration from the neighbouring patch, probably comprising mobile adults (straight arrow) and by larval immigration (curved arrow), patch C experiences a biological disturbance in the form of a megafaunal browser, and in patch B, one species is beginning to show dominance.

At time T_3, patch A is showing signs of recovery with a mix of species and fairly high evenness. Patch C undergoes recolonisation by adult and larval immigration, as occurred earlier in patch A. Patch B is demonstrating increasing dominance by one species. At T_4, the three patches form a mosaic of species richness and abundance, with no two patches

Figure 2.4 Grassle's Spatio-temporal Mosaic Theory (taken from Paterson, 1993). The figure shows three patches, A, B and C and a series of disturbances affecting them. The histograms associated with each patch represent the abundance of species, each block representing a different species (see text for detailed explanation).



showing identical patterns of diversity. This forms the heart of the spatio-temporal mosaic theory; within a small region, a high number of species can be maintained at disequilibrium, each patch experiencing disturbance events independently of each other.

Finally at T_5 patch B experiences a disturbance from a food fall - in this case wood, which attracts different species from the surrounding regions. These then contribute to the species pool of this region. This figure helps to demonstrate how, on a small scale, ecological processes may operate to maintain the species diversity of a particular area, at the maximum allowed by the environmental parameters.

The other main theory, the *Grain-matching Model,* was proposed by a number of workers (Jumars, 1975; Jumars, 1976; Jumars and Gallagher, 1982; Jumars and Ekman, 1983) to explain high diversity in deep-sea sites, according to equilibrium-based theories. Patterns of species diversity within the infauna were thought to occur as a consequence of biological interactions at the scale of the individual. Low-level physical disturbance was a common feature of their chosen study sites; for example, current speeds in the San Diego and Santa Catalina Basins rarely reach above 7cm s^{-1} (Jumars, 1975; Jumars, 1976) and yet diversity was much higher than predicted by the Intermediate Disturbance Hypothesis. The reason for this apparently anomalous observation was thought to be related to the scale of interactions. Much of the environmental heterogeneity was found to occur on the scale of biological influence, or the 'ambit' of individual organisms (Jumars, 1975; Jumars, 1976; Thistle, 1979; Thistle, 1983), such as locomotory range or spread of feeding tentacles. Jumars (1975; 1976) suggested that individuals were randomly distributed and the activities of a particular individual affected those around it, creating local heterogeneity. For example, the cirratulid polychaete, *Tharyx luticastellus,* produces a mud ball dwelling that has an inhibitory effect on a paraonid polychaete, yet enhances populations of certain meiobenthic copepods (Thistle and Eckman, 1988). Consequently, high diversity could be maintained locally by random species distributions generating many types of interactions such as these.

In the Spatio-temporal Mosaic Theory, biological interactions are not perceived as being able to maintain high diversity. However, Jumar's theory is not completely incompatible with this and the Intermediate Disturbance Hypotheses. In the Spatio-temporal Mosaic Theory, biological interactions are viewed as important following the creation of a patch.

From here it is but a small step to concede that biological interactions would increase in importance if disturbance became less frequent or intense.

It would seem then, to summarise, that both physical disturbance and biological interactions are important in generating environmental heterogeneity. The relative contributions of each can be considered to exist along a gradient, whereby as disturbance diminishes in size, frequency or intensity, then biological interactions increase in significance and patch size is effectively reduced to the size of the individual.

2.3 Patch-generating Processes in Marine Sediments

Grassle and Morse-Porteous (1987) suggested that the most important features of the deep-sea environment that determine community structure are likely to be:

(1) the spatio-temporal patchiness of organic input against a background of low productivity;

(2) sporadic, small-scale disturbance events occurring against a background of relative constancy;

(3) the lack of barriers to dispersal among populations distributed over vast areas of seafloor i.e. the open populations of Roughgarden (1986)

2.3.1 Patchiness Arising from Input of Organic Material

Until relatively recently, the general opinion was that the bulk of the energy requirements of deep-sea benthic communities was met by a sparse, steady drizzle of slow-sinking, small particles from productive surface waters. That view is now challenged by the plethora of evidence that rapidly sinking particles, either in the form of carcasses of nektonic animals or aggregated detritus, contribute significantly to the energy budget of these communities.

Smith (1985b; 1986) reported a significant attraction of eleven epibenthic, scavenging species, following deployment of nekton carcasses of varying sizes in the Santa Catalina Basin. Hagfish, penaeid shrimp, ophiuroids and amphipods were among fauna that

migrated to feed on the carrion. Although earlier work suggested that some 11% of measured, benthic community respiratory requirements was met by the energy flux in nekton falls (1983), the occurrence of carcasses in the Santa Catalina Basin is rare, accounting for a calculated 0.05 to 10% of the basin floor. Smith (1985b) concluded that, at least for the Santa Catalina Basin, "large food-falls represent an insubstantial source of disturbance-induced heterogeneity."

Other large food falls encountered include plant material of terrestrial origin such as wood, leaves and fruit, and also pieces of shallow-water seagrass and *Sargassum* (see Gage and Tyler, 1991). Of two sites studied on the Demerara Abyssal Plain, one received a significant input of terrigenous material from the Amazon River (Sibuet *et al*, 1984). Nematode assemblages at this site were found to be significantly more aggregated corresponding to the patchiness of the plant material than at the second site that received no input.

Similarly, macrofaunal diversity was observed to increase in those areas of sediment underlying patches of decomposing *Sargassum* weed, at an abyssal site off New England (Grassle and Morse-Porteous, 1987). Deliberately-deployed pieces of wood were also found to enhance diversity, although on these occasions, the colonisers were primarily wood-boring species unknown from the surrounding infaunal communities (Turner, 1973,1977).

Soon after the discovery of the significant, rapid, vertical transport of phytoplankton aggregates to the deep-sea floor (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986), Gooday (1988) documented the first evidence of a meiofaunal response to low-intensity enrichment such as this. Foraminiferal assemblages were demonstrated to migrate into the phytodetrital aggregates and subsequently undergo rapid reproduction. Grassle (1989) predicted that seasonal deposition of phytodetritus would increase the patchiness of benthic animals by increasing the heterogeneity of the environment. Lambshead and Gooday (1990) tested this theory using variability in foraminiferal assemblages and concluded that heterogeneity was significantly increased following the phytodetrital pulse.

Whilst phytodetrital material sinks and may arrive at the seafloor as a uniform covering, resuspension by bottom currents, and the topography of the seabed, concentrates material around mounds and in depressions, resulting in a patchy distribution on a scale of centimetres to tens of centimetres, that persists for at least months, if not from year to year. The patchy distribution of a holothurian, *Benthogone rosea*, was thought to reflect this patchy distribution of the phytodetritus (Rice *et al.*, 1986). Relict animal burrows are also implicated in increasing patchiness further by trapping and collecting material (Aller and Aller, 1986). Meiofaunal and bacterial abundances were two or three-fold higher in surface sediments surrounding abandoned ampharetid polychaete burrows.

2.3.2 Biologically-Generated Patchiness

Suspension feeders are dependent upon food being carried to them and consequently they can survive only where local hydrographic conditions permit. Unlike most shallow-water environments where there are major local variations in near-bottom currents, in the deep sea currents are generally slower and more predictable, and hence suspension and resuspension of particulate material is less common. As a result, suspension feeders are generally less abundant with increasing depth. Where they do occur in any numbers, their distribution is usually very restricted. For example, a hexactinellid sponge, *Pheronema carpenteri* was found in very high densities in the Porcupine Seabight (NE Atlantic), but within a very narrow bathymetric range between 1000 and 1300m (Rice *et al*, 1990). The sponges were found to occur where areas of the seabed were almost completely covered by a mat of sponge spicules. Macrofaunal samples collected from within this hexactinellid zone were found to have increased abundance and diversity than in surrounding areas where the spicule mat was absent. Bivalve and ophiuroid species were especially abundant, although gastropods, in particular, showed reduced representation in the samples (Bett and Rice, 1992). Whilst it is possible that the macrofauna and sponges were responding to some common variable, it was hypothesised that the spicule mats were responsible. This may be due to the mats increasing surface roughness and near-bed turbulence and hence disrupting the viscous sub-layer, or by trapping and concentrating suspended organic aggregates.

Another example of biologically-generated environmental heterogeneity was reported by Gooday (1984). He documented the use of rhizopod tests by numerous metazoans, primarily by sipunculans, polychaetes and nematodes. Subsequent studies (Levin *et al.*, 1986; Levin and Thomas, 1988) indicated a much wider diversity of inhabitants of xenophyophore tests in the eastern Pacific. Seventy per cent of the inhabitants were nematodes and harpacticoid copepods. Dominant macrofaunal inhabitants were ophiuroids, flabelligerid polychaetes and hebefustid isopods. It was concluded that xenophyophores contribute small-scale heterogeneity to community patterns in deep-sea sediments.

2.3.3 Patchiness Generated by Physical Processes

Physical disturbances in the deep-ocean environment may be generated on a small, localised scale by the vigorous feeding activities of scavengers attracted to nekton carcasses (Smith, 1986). Sampling sites in the Santa Catalina Basin were positioned to determine the disturbance and enrichment effects on infauna at various distances from deployed bait. Time-lapse photography indicated that the feeding behaviour of the scavengers caused a dramatic disturbance effect, eroding the top layers of sediment within a 50cm radius of the carcass. Although no enrichment effects were noted, some evidence for exploitation of these patches, by colonising species rare in the ambient communities, was documented. Smith (1986) concluded that such low intensity, small-scale disturbances must be common in the Santa Catalina Basin. As a result, in conjunction with low recovery rates of the infauna, much of the basin floor must be in disequilibrium, and hence such processes might structure the infaunal communities.

Construction of mounds on the sediment surface by burrowing invertebrates was also demonstrated to have a disturbance effect by burying the infauna (Smith *et al.*, 1986; Kukert and Smith, 1992). However, following deployment of artificial mounds, rapid recolonisation indicated that faunal assemblages in these areas could respond quickly to disturbance from echiuran mound building.

The complex effects of bottom currents were demonstrated, following a number of studies at the HEBBLE site on the Scotian Rise (NW Atlantic). Frequent (several times a year),

high energy (daily average current speeds of >20cm s^{-1} for several days) storms scour the top 1-2cm of sediment and subsequently redeposit the sediment as a layer of mobile mud after the storm has abated (Hollister and Nowell, 1991). The abundance of meiofaunal harpacticoid copepods was observed to be an order of magnitude lower immediately after such an event although recovery was rapid (occurred in weeks) (Thistle, 1988). Consequently Rice and Lambshead (1994) proposed that this high energy disturbance should reduce the patchiness of nematode and macrofauna assemblages ('blurring'). However, with the exception of the isopods, all macrofaunal and meiofaunal taxa were significantly ($P < 0.05$) aggregated and abundance was higher than at other deep-sea sites experiencing a less vigorous hydrodynamic regime. It was suggested that the benthic storms were releasing resources, hence enhancing food availability, and that this extra food was maintaining patchiness (Rice and Lambshead, 1994).

At a deep abyssal site in Setubal Canyon off Portugal, rippled bedforms contained dense aggregations of bivalves (Gage *et al.*, 1995; Lamont *et al.*, 1995) that were thought to have accumulated as a result of high hydrodynamic activity, as indicated by the sand ripples. At a nearby site on the Tagus Abyssal Plain, no such bedforms and no faunal aggregations were observed.

Animals producing biogenic structures (Jumars, 1976; Aller and Aller, 1986; Schaff and Levin, 1994) may also act as agents of physical disturbance in the deep sea. That is, they cause sporadic events within a discrete area that results in the mortality of local populations, as well as generating space for colonisation. However, Thistle (1983) found no correlation between harpacticoid distributions and biologically-created habitat heterogeneity at the HEBBLE site. This may be due to the strong physical regime acting as a controlling factor, and illustrates the need to assess all disturbances influencing a particular site (Pickett and White, 1985).

To summarise, the three ecological processes proposed by Grassle and Morse-Porteous (1987) operate best in relation to the low productivity, relative environmental constancy and large surface area of the deep-sea environment (Sanders, 1968; Osman and Whitlatch, 1978; Abele and Walter, 1979). Patchiness in organic input is more likely to be a significant feature of the environment against a background of low productivity (Jumars,

1976), and the effects of patchy disturbance will be more persistent in constant environments as the mosaic created by earlier disturbances is not destroyed (Jumars, 1976).

Large numbers of rare species contribute heavily to local diversity in the deep sea (as indicated by the high numbers of 'singletons' occurring in samples), but these species may not be viable in every microhabitat. For example, wood-borers require patches of wood, but can survive in surrounding sediments that cannot support viable populations of these species (Grassle and Morse-Porteous, 1987). The lack of barriers to dispersal over very large areas enhances the number of source populations, i.e. increases diversity (Osman and Whitlatch, 1978), as a result of these 'open' populations. The importance of open populations in the deep sea will be considered in greater detail in the next section.

2.4 Colonisation of Marine Sediments

2.4.1 Reasons for Colonisation of New Patches

Thistle (1981) and Thistle and Eckman (1988) proposed that species may respond to newly-disturbed patches for one of three reasons: (a) for release from interspecific competition, (b) for release or reduction of predation pressure and (c) for the release of a resource not normally available in the background environment.

Release from interspecific competition was the primary mechanism underlying the non-equilibrium theories of Connell (1978) and Huston (1979). Disturbance prevents or slows the approach to competitive exclusion by reducing competitive pressure. Grassle and Grassle (1974) proposed that a suite of species could be identified in soft-bottomed communities that could rapidly occupy newly-disturbed areas, then reproduce quickly to utilise resources before other competing species could exploit the new habitat. At this point the initial colonisers disperse in search of new habitats. The polychaetes, *Capitella capitata* and *Streblospio benedicti,* and the amphipod, *Ampelisca atennuata,* were said to be typical of such organisms within the macrofauna, being dramatic exploiters of new areas (Grassle and Grassle, 1974; Whitlatch, 1980). Extreme colonisers within nematode

communities are represented by the Rhabditidae, Neodiplogasteridae and the Monhysteridae (Bongers *et al.*, 1991). All of these species are often small, with a high colonisation ability, short generation times (as little as a few days for some nematodes), voluminous gonads, are often viviparous or egg brooders, and live in ephemeral habitats.

Release from competition was also the chief pathway invoked to explain succession in equilibrium theories (Grassle and Sanders, 1973) and led to the concept of *r*-species or opportunists. Caswell (1982) demonstrated that the use of terms such as 'opportunists' and 'competitors' was still valid within the boundaries of the Non-equilibrium Paradigm, but could no longer be used to predict where a particular community may be found upon the successional pathway.

The release-from-competition hypothesis was rapidly accepted as the primary reason for colonisation of newly-disturbed areas. It was invoked by Sousa (1984) to explain colonisation by algae on rocky shores, and similarly for the recruitment of bryozoans (Kay and Keogh, 1981; Keogh, 1984). In particular, small patches, such as the artificial settling plates of their experiments, were viewed as refuges from competition for grazer-resistant species.

In the deep sea, studies of the migrations of benthic foraminifera into phytodetritus aggregates indicated a clear response by some species but not others (Gooday, 1988). This was ascribed to phytodetritus aggregates offering living space free from competitors. Similar explanations were offered for the enhanced numbers of monhysterid and chromadorid nematodes also observed to respond to this dramatic organic input (Gooday and Turley, 1990; Riemann, 1995).

Nematode studies in shallow water indicated that increased organic load (Alkemade *et al.*, 1993), or stagnation of the deep waters in fjords that caused sediment anoxia and subsequent defaunation (Austen and Wibdom, 1991; Hendelberg and Jensen, 1993), were found to enhance the abundance of particular species. Dominance by members of the *Sabatieria* genus, in particular, occurred rapidly, suggesting exploitation by opportunists. Many of these species are known to be tolerant of low oxygen conditions and anoxia

(Wieser and Kanwisher, 1961; Jensen, 1986). Another opportunist common in areas of high organic loading is *Diplolaimella*, a monhysterid nematode (Lambshead, 1986).

Aggregations of *Pontonema vulgare* were observed around dead and moribund remains in an organically-polluted estuary, where the majority of other fauna had suffered high mortalities (Lorenzen *et al.*, 1987). These aggregations were so dense that the underlying sediments could not be seen. Samples were found to contain more than 50% juveniles suggesting a classic opportunistic response. Whilst it could be argued that this was, in fact, a response to the release of resources, replacement of the overlying water with oxygen-rich water was correlated with the rapid disperal of the aggregations. *P.vulgare* did remain in the ambient communities, albeit at considerably reduced numbers.

A similar model, originally proposed by Robles (1982), suggested that the second advantage of exploiting disturbed areas lies in subsequently-reduced predation. A prey-species individual experiences a reduced mortality rate by occupying a newly-disturbed patch until its predators accumulate, at which time it emigrates to a new patch. Robles studied the macrofauna of hard substrates and Sousa (1984) also utilised this theory for colonisation of large patches by algae, where grazing pressure would be much reduced.

In the deep sea, Thistle and Eckman (1988) suggested that predation-reduction might be responsible for close association of a harpacticoid copepod with mud balls constructed by *Tharyx* (a cirratulid polychaete). A response by the paraonid polychaete, *Levinsenia oculata,* to hexactinellid sponge spicules (Jumars, 1976; Jumars and Ekman, 1983), was proposed to occur as a result of predator inhibition, and similarly for the attraction of more than 12 metazoan species (including nematodes) found associated with agglutinating foraminiferan tests (Levin *et al.*, 1991a; Gooday *et al.*, 1992). Predator-exclusion experiments by Grassle and Morse-Porteous (1987) suggested that certain polychaetes found to behave opportunistically, were prevented from monopolising the sediments by predator cropping.

The mechanisms by which predators regulate prey populations include predator-induced disturbance, as well as consumption. Smith (1985b; 1986) found that, while scavengers responded to bait deployment, benthic infauna did not constitute a food resource for them.

However, frenzied feeding activities of the scavengers were sufficient to disturb a large area of sediment surrounding the bait, and with it, the infauna. In studies of fish predation upon benthic meiofauna, Palmer (1988b) also found that whilst nematodes did not constitute a significant part of the diet of the fish, they suffered dramatically-reduced densities due to displacement by feeding activities. In tidal sediments, the nematodes responded to submergence by downward migration within the sediments. Palmer concluded that this was an avoidance response, not to consumption, but rather to disturbance induced by feeding activities.

The final hypothesis concerning the reason underlying colonisation is that *disturbance releases resources* not otherwise available. By far the greatest body of work has been dedicated to the study of this hypothesis, especially in the deep sea, where one resource, food, is not readily abundant. In studies by Thistle (1981) and Varon and Thistle (1988), for example, food, in the form of enhanced microflora, was thought to be attracting assemblages of harpacticoid copepods to faecal mounds of the burrowing enteropneust, *Ptychodera*. Varon and Thistle (1988) demonstrated that this response could not be due to release from competition or predation, using experimental mounds devoid of fauna. Colonising harpacticoids showed no preference for these experimental mounds and, consequently, were argued not to be responding to provision of open space. In addition, the harpacticoids showed no preference for mound or ambient sediment when all organic differences were removed. Varon and Thistle proposed that faecal mound sediment, which contained a unique microflora, was the attractant for harpacticoids instead, i.e. disturbance was releasing a food resource.

Similarly, Warwick *et al.* (1988) noted a shift in the trophic structure of nematode communities in faecal mounds of the terebellid polychaete, *Streblosoma biardi*. Although density and diversity remained the same as in the ambient environment, they proposed that this shift in trophic assemblages represented a change in available resources. Higher bacterial numbers were thought to be that resource, reflected in the greater proportion of bactiverous nematodes and, correspondingly, their predators. In the Santa Catalina Basin, some spherical species of agglutinating foraminifera appeared to respond opportunistically to biogenic sediment mounds. Once again this was attributed to elevated bacterial numbers (Levin *et al.*, 1991a). Growth rates were accelerated compared to background levels.

In a comprehensive study of disturbance generated by feeding rays, Van Blaricom (1982) demonstrated that two amphipod species were disproportionately abundant in ray feeding pits. The ambient, near-surface infauna was displaced from pits made by feeding rays and the resulting shallow depressions trap drifting organic debris. Amphipods were not attracted to experimentally-dug pits that lacked this accumulation of organic material. The colonising amphipods were characterised by feeding predominately on organic matter at the surface and were therefore thought to be exploiting food resources accumulated in the ray pits. Oliver and Slattery (1985) observed a similar response for scavenging amphipods that were attracted to debris trapped in feeding pits dug by grey whales. Oliver and Slattery demonstrated experimentally that amphipods were more abundant in those areas of the pits containing debris.

A second type of data comes from studies of recolonisation of experimentally-placed trays of azoic sediment and other materials. Grassle and Grassle (1974) studied recolonisation of boxes filled with sediment, defaunated by freezing and thawing. In shallow sub-tidal sites in Massachusetts, the polychaete, *Capitella capitata,* increased rapidly to background densities, but the population crashed after two months. The decline was demonstrated to be neither a seasonal or predator-mediated event, but instead appeared to result from intraspecific depletion of resources.

Sediment tray recolonisation studies in the deep sea exhibit similar, if markedly slower, responses. After 26 months at bathyal depths near Bermuda (Grassle and Morse-Porteous, 1987), sediment trays had a faunal density that was an order of magnitude lower than background sediments, and similarly for recolonisation trays deployed in the Santa Catalina Basin at the same depths (Levin and Smith, 1984). Extrapolation of colonisation rates, to background levels of density and species richness, suggested that complete recovery may take two to five years (Smith and Hessler, 1987).

Of greater interest, in this context at least, is that the trays almost invariably contained a significant abundance of species rare or absent in background communities (Grassle, 1977; Desbruyéres *et al.*, 1980; Levin and Smith, 1984; Snelgrove *et al.*, 1992). These respondents often come from polychaete families well-known for their opportunism in

shallow waters. The trays represent a disturbed environment containing potentially more organic material from organisms killed then decomposing during the freeze-thaw process (Thistle, 1981; Snelgrove *et al.*, 1992). In addition, species abundant in background communities were often present in considerably reduced numbers in the recolonisation trays.

The existence of opportunists in the deep sea is most strongly demonstrated by the rapid colonisation of blocks of wood placed on the sea-floor. Wood is thought to be an especially uncommon resource in the deep-sea (Grassle and Morse-Porteous, 1987), yet despite this, artificially-deployed blocks are quickly colonised (11 months) by wood-boring species known exclusively from the deep-sea (Turner, 1977), that are absent from ambient sediments. This reflects, in part, the importance of a lack of barriers to dispersal upon the regional species pool. The huge, uninterrupted expanses of the deep sea may act to increase the numbers of potential colonisers, that may also have a positive effect on local diversity.

Sediment trays artificially enriched with *Sargassum, Macrocystis* or fish flakes, whilst demonstrating a clear colonisation response, also showed that colonisers, at least in the deep sea, are not ubiquitous and may vary according to the *type* of organic enrichment (Desbruyéres et al, 1980; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987). However, Smith and Hessler (1987) argued that the identities of tray colonisers depended upon the patch structure of the surrounding community. Trays enriched with *Macrocystis* flakes actually appeared to deter colonisation by most infauna, with the exception of a few nematodes (Levin and Smith, 1984). It was thought that toxic phenolics in the kelp might have been released during deployment, thus discouraging colonisation.

Care should be taken, however, when interpreting these results. As Smith (1985a) highlighted, sediment-tray recolonisation studies are prone to a number of experimental artefacts, relating to (a) alteration of hydrodynamics; (b) substrate isolation and (c) arbitrary sampling in space and time. Alteration of sediment-water interface hydrodynamics occurs because the sediment trays (with the exception of later studies following Smith's critique) protrude above the seafloor, thus altering the near-bottom flow. This may subsequently affect recruitment of swimming and passively-settling larvae .

(Eckman, 1983; Jumars and Nowell, 1984) and the flux of suspended particles, and the changed fluid dynamics may also alter bacterial growth in surficial sediments (Jumars and Nowell, 1984). Consequently, larval recruitment, growth and survivorship may be heavily biased. Additionally, substrate isolation eliminates all benthic modes of colonisation, which is an important consideration in deep-sea studies where larvae are often benthic and adults may be rarely suspended. Furthermore, colonisation is very patch-size sensitive (Smith, 1985a) and yet sampling has occurred at arbitrary intervals in space and time, i.e. population explosions and crashes may well have been missed.

In a comparative study, Smith and Brumsickle (1989) examined recolonisation of plugs of azoic sediment that were either flush with the sediment surface, or raised above it, in the manner of earlier colonisation tray experiments. Recolonisation was found to be much slower in the raised plugs and the contribution made by larval recruitment was also considerably reduced.

To conclude, from the studies described above, it would appear that no one hypothesis can be accepted over and above all others i.e. there is no generalised pattern of colonisation and opportunistic species may, in fact, be responding to a combination of competition-predation-resource events during colonisation of newly-disturbed patches. However, it *is* clear that opportunistic or fugitive species do occur in the deep sea, although they have been better described from the macrofauna than the meiofauna, and nematodes in particular.

2.4.2 Colonisation Modes in Soft Sediments

The arrival mode of initial respondents to patch-generating processes is a key aspect of colonisation, as it influences subsequent community development within that patch. For example, post-larval colonisation will create adult-adult interactions, whereas larval recruitment will generate larval-adult interactions. As these interactions are fundamentally different, the community that develops as a result will also be distinct. Levin (1984) proposed, for example, that distribution and abundance patterns of polychaetes in mud flats in Mission Bay, California, reflected developmental modes, dispersal and type of colonisation ability.

Smith and Brumsickle (1989) hypothesised that colonists may enter a disturbed patch by one of three modes: (a) settlement of pelagic larvae from the water column; (b) reproduction within the patch by species with benthic development, and (c) immigration of benthic juveniles and adults from surrounding sediments. However, as they correctly pointed out, a lack of life-history information for most benthic infauna makes it difficult to separate the first mode from the second, and so they are often merely distinguished from immigration of juveniles and adults.

The colonisation response can be divided into two main types; long-distance dispersal adapted for large-scale disturbances (>100m^2) and rapid colonisation in response to small-scale disturbance. These two responses will be considered in turn, but it remains to be highlighted that, between these two extremes of colonisation response, exists a range of combinations of the two modes.

2.4.2.1 Colonisation of Large-scale Patches

Studies of recolonisation following large-scale disturbance in soft bottoms are relatively few, for macrofauna and meiofauna alike. Studies have generally concentrated on recovery from anoxia events and disturbance generated by benthic storms.

Following an anoxic kill-off in low energy, fine sediments, recolonisation by macrofauna of trays mounted off the bottom suggested that larvae, particularly polychaetes, were the principle colonisers (Santos and Simon, 1980). However, the experimental design did preclude migration of adults. Studies of the recovery of soft-sediment communities following an oil spill event off Massachusetts confirmed the role of larvae as primary colonisers, despite the water-column dispersal abilities of many benthic species' post-larval stages (Sanders *et al.*, 1980).

Nematode populations recovering from a similar anoxic event in the Gullmar Fjord, Sweden, contained a disproportionately high abundance of juveniles (Austen and Wibdom, 1991). Nematodes generally lack a planktonic dispersal phase in their life-histories, so this may represent reproduction by opportunistic species tolerant of low oxygen levels, rather than immigration from surrounding unaffected areas.

In the deep sea, benthic storms experienced on the Scotian Rise (NW Atlantic) periodically erode surface sediment layers over huge areas, redepositing the sediments later during periods of quiescence. Analysis of the macrofauna (Thistle *et al.*, 1985) indicated that polychaetes and bivalves, collected from a site experiencing such storms, contained smaller individuals than at other deep-sea sites and no sexually-mature individuals were found. Thistle *et al.* (1985) suggested that larvae were responsible for recolonisation of patches created by these storms and adult migration was thought to be low. A similar observation was later made for harpacticoid copepods (Thistle, 1988) but not for nematodes (Thistle and Sherman, 1985). Once again, this was attributed to the lack of a planktonic dispersal phase in nematodes, but also the ability to mitigate the effects of the storm by burrowing deeper in the sediments.

2.4.2.2 Colonisation of Small-scale Patches

Within the macrofauna, studies of colonisation of small-scale patches indicate that, in the main, this occurs by post-larval and/or adult immigration from neighbouring sediments. In Mission Bay, California, the coloniser size-frequency distribution was always positively skewed i.e. juveniles were the primary colonisers, even though all stages in the life histories (larvae, juveniles, adults and brooding adults) were available for colonisation (Levin, 1984). Brooding adults also made an important, though not significant, contribution. Two spionid polychaete species, however, did exhibit long-range dispersal potential with planktonic, seasonally-available larvae. Irrespective of colonising stage, in this study all primary colonisers arrived via the water column.

In a study of nematode and harpacticoid colonisation of ray feeding pits, however, no disproportionate response in abundance occurred during recovery (Reidenauer and Thistle, 1981; Sherman *et al.*, 1983). Whilst feeding pits may accumulate organic debris, they did not appear to be acting as catchments for either of these taxa, suggesting that in-water migration was not the primary means of colonisation.

Similarly, in Smith's (1985b; 1986) studies in the Santa Catalina Basin, recovery of infauna around baitfalls, following sediment disturbance by scavenger feeding activities, occurred primarily by in-sediment migration of adults, especially amongst colonising

polychaetes. Upward burrowing and horizontal migration were also thought to be the principle mechanisms underlying colonisation of echiuran faecal mounds in shallow water (Kukert and Smith, 1992).

'Olafsson *et al* (1990) examined the effects of faecal mounds, generated by the ampharetid polychaete, *Melinna palmata,* on copepods and nematodes. Whereas nematodes showed no significant change in abundance, diversity, trophic or community structure, one species of benthic copepod displayed a disproportionate abundance in the faecal mounds, when compared with ambient sediments. Furthermore, high proportions of both adults and juveniles were found in the water column overlying the sediments. The rapid response of a harpacticoid copepod to enteropneust faecal mounds was similarly attributed to the presence of adults in the water column (Varon and Thistle, 1988). A lack of response by nematodes to newly-created patches was also observed following phytodetrital deposition in the Porcupine Seabight (Gooday *et al.*, 1996), contrary to previous findings (Thiel *et al.*, 1988/89; Riemann, 1995). No obvious migrations were observed and nematodes were conspicuously absent from phytodetrital patches.

This absence of a colonisation response by nematodes to newly-created patches may be explained by considering the colonisation modes utilised by macrofauna, namely by upward or lateral burrowing, or via the water column. Post-larval movements can be considered as a series of small steps, whose length is proportional to the size of the animal. Smith and Brumsickle (1989) inferred that, for certain polychaete post-larvae, if this step-length was greater than the patch radius, colonisation by migration could be assumed to be relatively simple and rapid. If average nematode body length (in the deep-sea) is less than one millimetre, this would correspondingly infer a much shorter step-length and, therefore, migrations would cover much smaller distances or take greater periods of time.

Riemann (1995) investigated the reason for the almost universal lack of response by nematodes to a phytodetrital layer. The wave-like undulations of nematodes can only generate progression if the waves exert force against an external resistance. Experimental aggregations of a monhysterid species were observed to preferentially occur around and in small lumps of dense agar added to seawater (Vranken *et al*, 1981). Riemann argued that, like seawater, detrital material offers minimal external resistance. However, mucus-

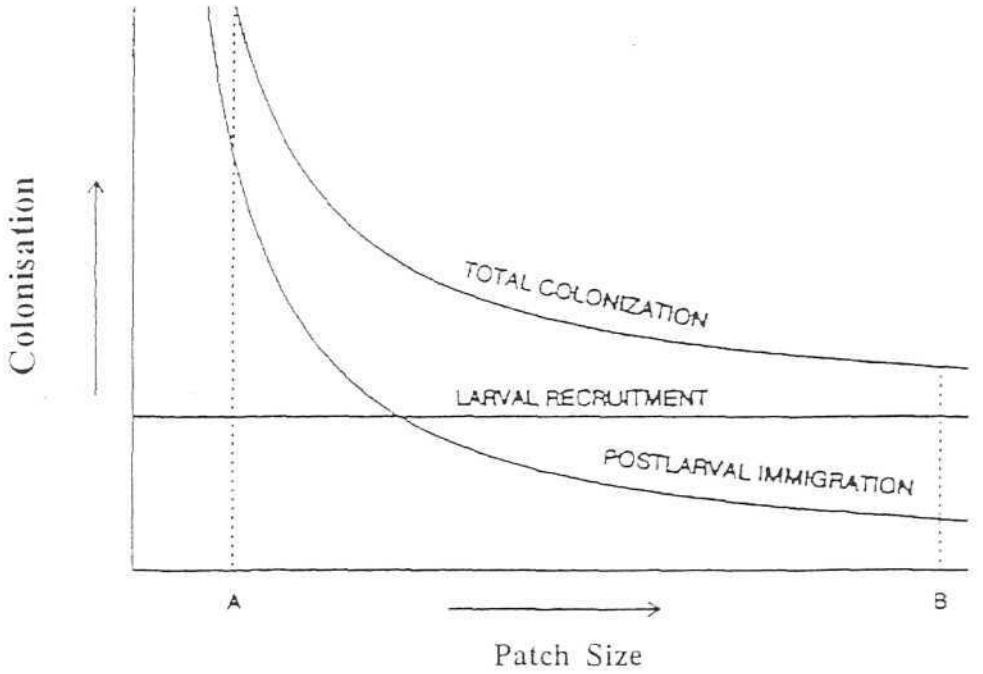
secreting nematodes may be able to condition the detrital environment using their mucus to agglutinate particles, facilitating locomotion. Bussau (1993) found that certain nematode genera, *Monhystera* (*c.f. Thalassomonhystera*) being among them, produce mucous tubes and amorphous sediment agglutinations. This may explain the response of *Thalassomonhystera* individuals to phytodetritus that was recorded by Riemann (1995).

In addition, unlike harpacticoids which are relatively good swimmers, nematodes are rarely found in the water column. Since they possess only longitudinal muscles, most species are poor swimmers and generally avoid surficial sediment layers. Some may even migrate downwards during periods of water movement (Palmer, 1988a). Chandler and Fleeger (1983) demonstrated, in a series of experiments that, generally, colonisation by copepods occurs almost entirely via the water column, whereas nematodes rely on infaunal movement. Water-column dispersal of nematodes from mudflats was found to occur primarily by passive erosion (Palmer and Gust, 1985), although only 5% of the total sediment community was suspended over a tidal cycle. Studies have shown that greatest concentrations of nematodes in the water column are highest when frictional velocity is high (Hagerman and Rieger, 1981; Palmer and Gust, 1985). Frictional velocity is an expression of shear stress, or the erosive force imparted by flowing water on the bottom sediments and fauna therein i.e. it is a passive transport mechanism. Juveniles of a *Metachromadora* species were found to be disproportionately abundant in the water column (Eskin and Palmer, 1985), which would suggest increased opportunities for colonisation of new patches, but actual settlement and subsequent establishment have not been well studied.

Smith and Brumsickle (1989) presented a conceptual model to illustrate the interactions between larval recruitment, post-larval immigration and patch size and their effects on average colonisation rate, for a single benthic infaunal species with planktonic larvae (Figure 2.5). The patch-size sensitivity of post-larval immigration reflects the small distances of post-larval movements relative to the radius of the patches. However, larval recruitment rates were thought to be independent of patch size, perhaps because larvae are transported as suspended load. At some threshold patch size, colonisation is dominated by immigration and similarly, there is a higher threshold where larval recruitment becomes important. The curves show the relative contributions of larval recruitment and post-larval

immigration to colonisation in patches of increasing size. Smith and Brumsickle stressed, however, that the curves would vary with locality, species, season and life history of the community. It would appear that the evidence presented here does support this general schema. The model would seem to be of key importance in low energy environments, where erosion and subsequent transport of macrofaunal adults and juveniles is rare. Based on existing evidence regarding nematodes, however, it is difficult to ascertain the relevance of the model to nematode communities, especially given that most nematodes generally lack a planktonic phase.

Figure 2.5 Smith and Brumsickle's (1989) conceptual model, showing the relative contributions of larval recruitment and post-larval immigration to average colonisation rate, for increasing patch sizes, for a single species with planktonic larvae. Patch-size sensitivity to post-larval immigration is greatest between lines A and B.



2.5 Succession in Marine Sediments

According to the Equilibrium Paradigm, succession was a predictable sequence of species replacements, culminating in a determinable climax community. Under the constraints of non-equilibrium theories, however, this definition can no longer hold true. The hypotheses of both Connell (1978) and Huston (1979) predict that diversity and evenness would be low in areas where disturbance was low or ceased. Although this implies an endpoint community of some kind, in most communities disturbance resets the patch before a stable endpoint can be reached. Theoretically it is possible that an end point could be achieved (Huston, 1979), but it is uncertain whether it would be either predictable, or the result of a successional pathway.

For marine sediments, few studies have addressed the succession issue. Van Blaricom (1982) found evidence for a successional sequence in the recolonisation of ray feeding pits, that culminated in a return to ambient community diversity, density and structure. However, in the deep sea, Smith and Hessler (1987) found no evidence in recolonisation tray experiments of a simple successional sequence. Similarly, during the recovery of nematode populations from an anoxia event, Austen and Wibdom (1991) could find no predictable pathway of recovery; indeed, communities never returned to a 'climax' fauna that resembled their original natural state.

These results suggest that succession is difficult to separate from normal community dynamics. Furthermore, without knowledge of the disturbance history of a sampling site, it is difficult to predict where, on a successional pathway, an assemblage might be. Formerly, according to equilibrium theory, it was possible to predict the stage in succession of an assemblage by examining the species life-histories. A patch would be in the early stages of succession if the community was dominated by opportunistic species and would be at a later stage in the succession if competitors dominated. It has already been explained why this approach is flawed, due to the difficulty in assigning accurate life histories, but it is also influenced by co-existence (especially in the deep sea) of *r* and *K*-species in new patches (Smith and Hessler, 1987), and the persistence of opportunists at all times with no obvious succession (Levin, 1984).

With an understanding of the disturbance history and the community structure of a particular site, an acceptable definition of succession within the boundaries of dynamic equilibrium theory could become:

> *"the return of a patch to within the normal ranges of diversity, density and species composition of the ambient fauna"* (Paterson, 1993)

Although acceptable, this definition generates yet more questions. In high diversity environments or those high in habitat heterogeneity it is difficult to describe the ambient fauna. Following this argument, it would also be difficult to assess what ranges of diversity, density and species composition could be considered as 'normal'. However many studies, especially those in the deep sea, were based upon experimentally-generated patches, thus the disturbance history would be known and successional changes could be studied.

Connell and Slatyer (1977) proposed that there were three major processes structuring succession: inhibition, tolerance and facilitation. Inhibition results from the activities of an individual that hinders the recruitment of other individuals to its immediate vicinity. This mechanism describes the dominant mode of succession on hard substrates (e.g. Paine and Levin, 1981).

According to the tolerance model, any species can occupy any unexploited gap in the environment, but there is a distinct hierarchy of species-by-species replacements based on competition or tolerance to environmental conditions, e.g. the succession of nematode communities following a return to oxic sedimentary conditions in the Gullmar Fjord, Sweden (Austen and Wibdom, 1991). McCall (1977) also attributed some soft-bottom succession to tolerance of later successional species. This appears to be the most common form of succession in soft-bottom communities.

Facilitation is the modification of the environment by species, such that it enhances the settlement of other species whilst hindering their own recruitment or self-replacement. This ensures community change, as species subsequently become extinct from a patch. Facilitation was deemed to be the most important process in Skagit mud flats (Puget

Sound, Washington), as deposit-feeders altered the sediments by building tubes and depositing faecal pellets. Early colonists, such as *Tanais* sp. and the bivalve *Macoma balthica,* encouraged recruitment of polychaetes such as *Hobsonia florida* and *Pseudopolydora kempi japonica*. This response overrode earlier theories of infaunal adults having a deleterious effect on the recruitment and survival of larvae and young juveniles (1982a; 1982b). Similarly, Woodin (1979) predicted that tube builders would settle preferentially with other tube builders.

Facilitation can also be invoked to explain the attraction of harpacticoid copepods to faecal mounds of the enteropneust, *Ptychodera*. Modification of the sedimentary microflora was found to actively encourage settlement of at least one harpacticoid copepod species (Varon and Thistle, 1988). Similar modification may also be the cause of nematode attraction to the burrows of the soldier crab, *Mictyris platycheles,* in intertidal sand-spits on the Tasman Peninsula (Warwick *et al.*, 1990a).

Nevertheless, there is also evidence that inhibition is as likely as facilitation. A species may facilitate settlement of some species and yet also inhibit others. For example, in the Skagit mud flat study, *Macoma* inhibited settlement of *Tanais,* whilst encouraging settlement of *Hobsonia florida.* Weinberg (1979) found that activity of the maldanid *Axiothella* inhibited settlement of the spionids *Pseudopolydora kempi* and *Polydora ligni* by reducing surface organic material. Consequently, the spionids had to extend further out of their tubes to forage, increasing their susceptibility to predation.

Studies of succession in the deep sea indicate that recovery from disturbance events may take a long time. Smith and Hessler (1987) proposed that small-scale discrete patches would take two to five years to recover. However rates of recovery have also been observed to vary from site to site, making it difficult to predict what will happen following a disturbance event.

2.6 Conclusions

To summarise, drawing on the evidence given above, several remarks can be made regarding patch dynamics, colonisation and succession in the deep sea:

(a) Disturbance is a widespread structuring process which operates on a number of time scales and frequencies, and its agents can be physical or biological.

(b) The diverse range of disturbance experienced in the deep sea leads to generation of many different kinds of patches being created on a local scale.

(c) Colonisation is variable, depending on the time of disturbance, its size/magnitude and its frequency:

(i) smaller patches appear to be colonised by adults, but as patch size increases then larval recruitment becomes more important. For nematodes the relative contributions are difficult to assess, but adult/juvenile migrations would be expected to play an important role.

(ii) as disturbance frequency increases, only motile adults will be able to exploit patches. Often classical r-species are not involved in colonisation and equilibrium species might exist. This arises because disturbance frequencies are generally low and thus conditions within a newly-disturbed patch might fall within the tolerance range of both *r* and *K*-species.

(iii) the initial colonisation response does occur most often in response to release of a resource, although insufficient evidence exists to refute competition/ predation theories

(d) Little evidence has been recorded for a predictable successional pathway following colonisation. Rather, a number of potential outcomes are likely, based upon the species pool of the surrounding communities.

(e) Given that patches are created by different forms of disturbance and that colonisation and succession depends on the frequency, magnitude/size of disturbance, and the

regional species pool, no patch within the deep sea environment should be the same as any other, thus promoting heterogeneity. If so, then diversity will be high, as predicted by patch dynamics theories.

3.1 Experimental Procedures

3.1.1 Field Sampling

Samples were collected from four stations along the JGOFS 140°W transect (Figure 3.1) during the benthic leg of the US JGOFS equatorial Pacific process study in October-November, 1992. Sampling locations, water depths and collection dates are listed in Table 3.1. These particular sampling sites were chosen for the study because previous research indicated that they experience a gradient in the overlying surface primary productivity and associated POC flux, and sediment accumulation rate. However, they do display generally constant water depths, hydrodynamic regime and bottom-water oxygen concentrations (Murray *et al.*, 1992).

Additional samples were also collected from a fifth site, the US JGOFS Hawaiian Ocean Time-series (HOT) station (located at 22° 45'N, 158°W, 4750m water depth, Figure 3.1), station ALOHA, in August 1992. This location, in physical characteristics of the sea-floor, closely resembles the 9°N station. Station ALOHA is thought by some to be located under the oligotrophic North Pacific gyre and consequently is considered representative of much of the Pacific abyssal ocean basin that experiences a low organic carbon flux. Quantitative samples were collected by Dr Craig Smith of the University of Hawaii, using both a multiple-corer and a USNEL-type box-corer with vegematic inserts.

3.1.1.1 The USNEL Spade Box-corer

Hessler and Jumars (1974) developed the USNEL box-corer at the Scripps Institute of Oceanography, in conjunction with the United States Naval Electronics Laboratory (USNEL) at San Diego. This sampling gear, which has become standard use for the quantitative collection of smaller fauna, retrieves relatively undisturbed samples covering an area of 50 x 50 cm. Those samples collected by grabs are usually folded and an anchor dredge may mix the sediment completely as it must be dragged for a short distance before achieving full bite.

Figure 3.1 Sampling locations for the benthic leg of the US JGOFS study (modified from Smith *et al.*, 1996).

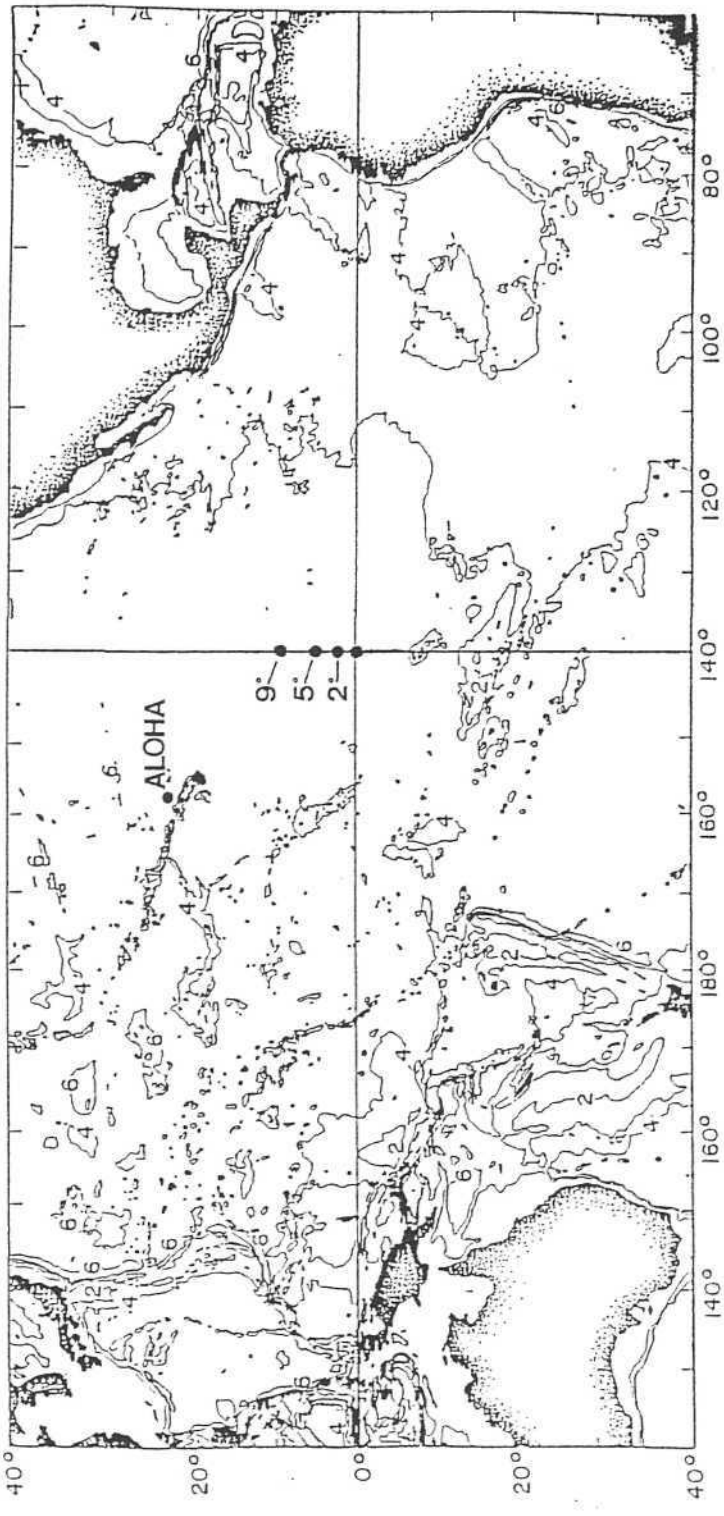


Table 3.1 Station locations, water depths and collecting dates for cores that were collected for meiofaunal analysis. The coring device used is also listed for each core.

Sample	Location		Water Depth (m	Date	Collecting Device
BC4	00°06.00'N	139°43.90'W	4328	15/11/1992	Box-corer
BC6	00°06.62'N	139°43.96'W	4305	16/11/1992	Box-corer
BC7	00°06.40'N	139°44.10'W	4307	18/11/1992	Box-corer
BC8	00°06.98'N	139°43.94'W	4301	19/11/1992	Box-corer
MC15	00°06.57'N	139°43.42'W	4304	19/11/1992	Multiple-corer
BC9	02°03.94'N	140°08.94'W	4409	20/11/1992	Box-corer
BC10	02°04.00'N	140°07.90'W	4414	21/11/1992	Box-corer
BC11	02°03.96'N	140°08.06'W	4409	22/11/1992	Box-corer
BC12	02°03.80'N	140°07.90'W	4410	23/11/1992	Box-corer
BC15	05°05.00'N	139°39.00'W	4447	27/11/1992	Box-corer
BC16	05°04.42'N	139°38.90'W	4446	28/11/1992	Box-corer
BC17	05°04.80'N	139°38.50'W	4424	29/11/1992	Box-corer
BC18	05°04.20'N	139°38.40'W	4320	30/11/1992	Box-corer
MC26	05°04.30'N	139°38.30'W	4418	30/11/1992	Multiple-corer
BC19	08°55.08'N	139°52.20'W	4986	03/12/1992	Box-corer
BC20	08°56.04'N	139°51.55'W	4994	04/12/1992	Box-corer
BC22	08°55.80'N	139°52.30'W	4991	06/12/1992	Box-corer
MC1	22°54.69'N	157°49.74'W	4880	29/07/1992	Multiple-corer
MC2	22°54.95'N	157°49.93'W	4871	29/07/1992	Multiple-corer
MC4	22°54.74'N	157°50.21'W	4880	31/07/1992	Multiple-corer
MC6	22°54.64'N	157°49.86'W	4884	01/08/1992	Multiple-corer

The box-core sample is divided *in situ* into 25 sub-cores with the vegematic modification of Jumars (1975). Each vegematic core has a plan area of 100 cm^2. The presence of vegematic sub-dividers minimises movement of the overlying top-water during core retrieval and hence reduces resuspension of the fine sediments and small fauna found at the sediment-water interface.

Following contact with the sea bed the rectangular box-core sinks into the sediment (Figure 3.2). It is guided by gimbals mounted on the supporting frame which ensure vertical sediment penetration, even when the frame lands on a sloping bottom. When the weight of the corer is released from the main hauling wire, the spade arm is released. As tension increases on the wire as the device is reeled in back to the ship, the spade arm is lowered into the sediment and closes the bottom of the corer. The top of the corer is closed with paired valves. These are left open during descent to allow water flow-through which acts to minimise a bow-wave effect as the device approaches the seabed. Further take-up of the wire pulls the device clear of the sediment.

The box-corer is lowered vertically from the ship at *ca.* 40m.min^{-1} until it is close to the bottom. Its position above the seafloor is monitored using a 12KHz benthos deep-sea pinger mounted on the wire, 12m above the box-corer. It will also detect pre-firing in the water column and confirm firing on the seafloor. When the sampler is approximately 100m from the bottom, its descent rate is slowed to *ca.* 20m.min^{-1}. This acts to reduce any bow wave effect and yet maintain sufficient speed for the apparatus to adequately penetrate the seabed and not 'skip' along the sediment surface due to movement of the ship. A wire metre attached to the main hauling wire detects the sudden drop in tension as the device reaches the seabed. A further 2-3 metres of wire are paid out before the winch is stopped. Retrieval begins at an initial rate of 15m.min^{-1} until a marked increase in wire tension indicates that the corer has broken clear of the seafloor. Retrieval then continues at a speed of 50m.min^{-1}. Once on deck the whole box-core, with its sample, is removed from the rest of the device so that the entire upper surface is exposed for inspection and manipulation.

A successful box-core sample was one that had retained its clear, cold, overlying water with an undisturbed sediment surface (Smith *pers. comm.*).

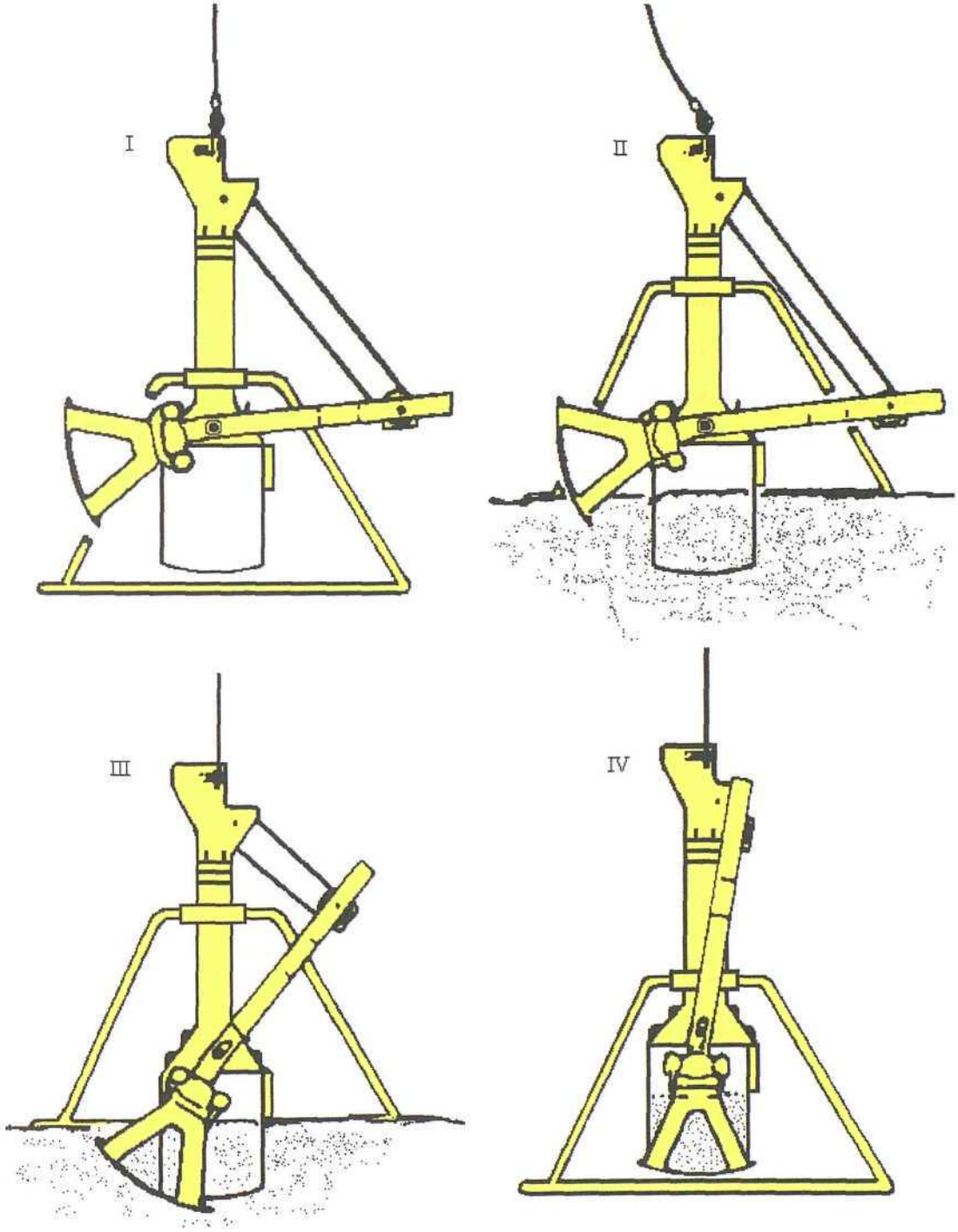
Figure 3.2 Diagram showing the deployment sequence of the USNEL Spade Box-corer (modified from Gage and Tyler, 1991).

I) Box-core ready for deployment

II) On bottoming, the core penetrates the sediment, releasing the locking plate for the spade arm

III) As the core is retrieved, the spade arm swings shut over the lower edge of the box

IV) The box is sealed and the gear is retrieved from the sea bed



3.1.1.2 The Adolf Wuttke GmBH Multiple-corer

This multiple-corer, based upon that developed at the Scottish Marine Biological Association (SMBA) is used to collect high-quality samples. Multiple-cores are virtually free of bow-wave-derived bias (Barnett *et al.*, 1984) and core disruption during recovery (Bett *et al.*, 1994). An outer framework supports a weighted assembly of eight core tubes (plan area of 80 cm^2) mounted under a hydraulic damper. When lowered, the frame rests on the seabed and the wire slackens. The coring assembly penetrates the seabed very slowly as a result of the damper. A ball mechanism seals the top and bottom of the core tubes to prevent loss or disturbance of the cores during recovery. The success of multiple-corers in collecting core samples, whilst maintaining their integrity, is testified by the sampling of easily-suspended phytodetrital floc in the deep Northeast Atlantic (Billett *et al.*, 1983; Rice *et al.*, 1986; Thiel *et al.*, 1988/89; Pfannkuche, 1993; Rice *et al.*, 1994) and in the central equatorial Pacific (Smith *et al.*, 1996).

Multiple-corer tubes and vegematic sub-cores were removed from the corers as quickly as possible following core recovery and sliced at vertical intervals (0-1cm, 1-2cm, 2-3cm and 3-5cm) with large aluminium cutting blades. Each section was transferred to a plastic screw-top container and immediately fixed in formaldehyde solution, diluted to 4% with seawater. Prior to this, the top-water from the cores was siphoned off and passed through a 63µm sieve and the residue added to the 0-1cm samples. As samples were collected by Prof. C Smith of the University of Hawaii, no decision could be made regarding isolation of the phytodetritus and associated fauna for analysis. Ideally, separation of this material would have allowed determination of the migratory behaviour into this habitat. Instead, this material was included in the 0-1cm sediment layer.

3.1.2 Sampling Design and Pseudoreplication

As seen in table 3.1, samples were collected by box-corer and multiple-corer at some stations but by only one type of gear at others. In a comprehensive, comparative study, Bett *et al.* (1994) demonstrated that the apparent density of meiobenthos, including nematodes, could vary by as much as 50% depending on sampler type. Previously, Thiel *et al.*. (1988/89) had noted that smaller amounts of detritus material overlying the sediments were recovered in box-core samples compared with multiple-core samples

taken in the NE Atlantic, and argued that this demonstrated the bow-wave effect of the box-corer. However, during a study in the NW Atlantic, Thistle (1983) and Thistle and Sherman (1985) found no evidence of a significant bow-wave effect on meiobenthic densities from sub-divisions of individual 'vegematic' box-corer samples. Bett *et al.* (1994) concluded that the bias attributable to sampler-type is likely to vary between taxa, the presence or absence of phytodetritus, or according to sediment type. Consequently, no general correction factor could be applied when comparing data from different samplers.

In the present study, the decision not to apply a correction factor was made based upon consideration of intra-station variability. For example, if multiple-core densities did not appear to be consistently greater than box-core samples, the use of a correction factor would be deemed inappropriate (see chapter 4, section 4.2.1). Whilst in ideal circumstances only samples from the same type of sampler would be considered, it was felt that in this case, the negative effects of removing one sample from 0 and 5°N and all samples from station ALOHA (e.g. reduced statistical power, loss of reference site) would outweigh the advantage of sampler uniformity. This strategy has been adopted by other authors in earlier meiofaunal studies (e.g. Boucher and Lambshead, 1995; Thistle *et al.*, 1995).

The decision to combine both sampling techniques may introduce an element of systematic error into the experimental design of this study. The next section will attempt to explain other sources of error that may be incurred in an experiment of this type.

Hurlbert (1984) recognised two types of ecological experiment, mensurative and manipulative. Mensurative experiments only involve measurements made at one or more points in space and/or time. Space or time is the only experimental "treatment" and forms the basis for the current study. Manipulative experiments always involves two or more treatments and the goal of the experiment is to compare the effects of these treatments. Its defining feature is that each experimental *unit* (the level in an experiment at which replication is obligatory) receives different treatments and the assignation of treatments can be randomised. As experimental manipulation plays no part in the current study, it will not be discussed further here.

As in the current study, mensurative experiments do not involve imposition of external factors by the experimenter. Although four stations along a phytodetrital gradient have been used, no manipulation was performed and, instead, nematode community properties were recorded from four points. Such an experiment was termed a *comparative mensurative experiment* by Hurlbert (1984). In experiments of this type, it is most important that replicate samples are dispersed (in space) appropriate to the hypothesis being tested.

In mensurative experiments, pseudoreplication often arises simply as a consequence of the choice of sampling locations. Generally, the actual physical space is less than the inferential space of the hypothesis. Pseudoreplication can be defined as "testing for treatment effects with an error term inappropriate to the hypothesis being considered" (Hurlbert, 1984). For example, in this study, an ideal sampling strategy would have seen samples collected from random points along the latitudinal line at each point on the transect. Instead, having samples from a fixed number of points along the transect merely provides information about the differences between those points, rather than along the gradient as a whole. If a significant difference were found in a particular property between sites, then it would be incorrect to interpret this as demonstrating a difference between latitudes. Pseudoreplication such as this is widespread in mensurative and manipulative experiments recorded in the literature (see review in Hurlbert, 1984).

Whilst an important point for the inference that can be applied to subsequent statistical analyses, it is important to bear in mind the difficulties associated with deep-sea sampling. Because of the great depths involved (5000m on average), and the expense incurred in ship-time, the best practicable option during deep-sea sampling is to choose a number of stations along a straight-line transect where the ship will remain stationary during sampling. Strategies such as this have been employed in meiofaunal studies in the deep sea by a number of authors (Tietjen, 1976; Shirayama, 1984a; Soetaert and Heip, 1989; Tietjen, 1992; Soetaert *et al.*, 1997), and consequently will be deemed acceptable in the current study. However, inferences made based upon statistical analyses will be treated with caution.

Other potential sources of 'confusion' in the present study include: (1) temporal changes – the nematode communities have been sampled only at one point in time and therefore can provide no information about possible seasonal effects etc. (2) Procedure effects – these will hopefully have been kept to a minimum by examining multiple samples from each station and similarly for experimenter-generated variability. (3) Experimenter bias – this may have been incorporated into the biomass measurements and identification. It was attempted to keep such bias to a minimum by 'randomly' selecting individuals when mounting slides (although it was anticipated that this might result in artificial selection according to body size and shape), with subsequent use of a random number generator to select slides to be examined (see sections 3.1.4 and 3.1.5).

3.1.3 Extraction

The sample to be extracted was washed with tap water into a 45µm sieve stacked on top of a 32µm sieve. Both sieve sizes were used initially, as previous research undertaken by the Nematode Research Group at the Natural History Museum, London, suggested that a potentially significant proportion of the nematodes within a sample may be lost through a 45µm sieve (Ferrero *pers.comm.*). The sample was rinsed thoroughly to remove all material smaller than 32µm and all traces of formaldehyde solution. The material retained in each sieve; nematodes, other meiofaunal organisms, and detritus along with some fine sand, was concentrated on one side of the sieve and left to drain for a short period. The extraction process used was the flotation method of De Jonge and Bouwman (1977) which employs the colloidal silica, Ludox-TM. The procedure was adapted slightly according to Ferrero (1992).

The 45µm sample was rinsed on the sieve using a Ludox solution that had been diluted with tap water to a specific gravity of 1.15. This rinsing occurred three times to remove any remaining water that would dilute the Ludox solution further. The sample was then washed into a 150ml plastic, screw-top container with Ludox solution. Separation of the fauna from other materials was achieved by allowing the samples to settle for a minimum period of 3 hours and a maximum of 18 hours. Less than this minimum value and complete separation did not occur; longer and separation appeared to break down. The 32µm sample was treated in an identical fashion.

After separation, the suspensions were poured off through their respective sieves, washed thoroughly with tap water and allowed to drain for a short time. They were each rinsed three times with distilled water to drive off any remaining tap water, and were then washed into separate, labelled petri-dishes with distilled water. Approximately 2ml of formaldehyde solution, diluted to 4% with distilled water, was added to each suspension. In this way the faunal material could be safely stored in the petri-dishes for up to one week, without risk of degradation. The settled sediment was resuspended in Ludox solution and the extraction process was repeated until no nematodes remained in suspension for three consecutive flotations.

The nematodes were hand-picked from the petri-dishes using an eyelash mounted on a wooden skewer (mounting 'needle') and were transferred to a 50 x 50 mm cavity block containing dehydration fluid. By removing nematodes individually, no debris contaminated the final sample, that may have obscured the fauna once on the slides, thus hindering identification. Picking was made easier and more accurate using a binocular dissecting microscope and marked petri dishes. These had been scored on the underside using a diamond pencil, with a series of horizontal lines to act as points of reference. Following these reference lines ensured complete examination of the petri dish and 100% removal of all nematodes. It also permitted a primary count of the numbers of nematodes per sample. The dehydration fluid comprised 5% anhydrous glycerol, 5% IMS alcohol and 90% distilled water (Seinhorst, 1959). Phenol crystals were added as a fungicide (Platt and Warwick, 1983).

After all nematodes had been transferred to the dehydrating fluid, the cavity block was covered, leaving a small opening to allow evaporation and placed in a dessicator. The water and alcohol were allowed to evaporate, leaving the nematodes in anhydrous glycerol.

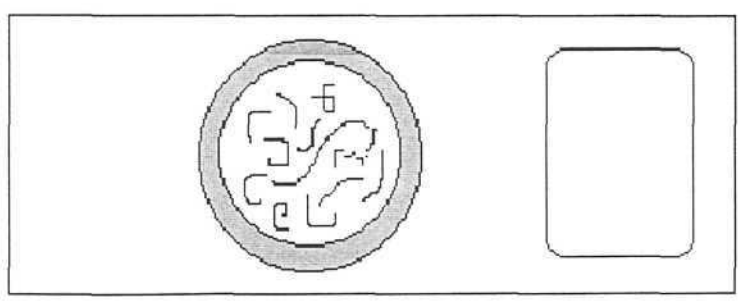
3.1.4 Mounting

Microscope slides were prepared with circular, paraffin wax rings of approximately 15mm diameter - slightly smaller than the diameter of the cover slips used. 76mm x 26mm slides

were washed in IMS alcohol and dried with a tissue to remove dust and oily residues. The paraffin wax was melted in a glass crystallising basin and the applicator (a short length of copper tubing with a wooden handle) was warmed to the same temperature. Optimum warming temperature was determined by trial and error. Once at temperature, the applicator was lifted from the wax and held against the centre of the slide for approximately 3 seconds, leaving a wax ring on the slide. Slides were prepared as needed to keep them free from dust prior to use.

A small drop of anhydrous glycerol was placed in the centre of the wax ring and 10-20 nematodes were transferred from the cavity block to this glycerol. Again the mounting 'needle' and a dissecting microscope were used to aid in picking the nematodes. Nematodes were chosen at random from the cavity block. A coverslip was carefully added, ensuring that it overlapped the wax ring all round. The slide was placed on a warm hot plate and the wax ring carefully melted, allowing air bubbles to escape. As soon as this had occurred, the slide was transferred to a level surface and the wax allowed to solidify. Details of the sample plus the slide number were recorded on a label on one end of the slide. The preparation was finished by sealing the coverslip with Gurr's glyceel and then left to harden for twenty-four hours (Figure 3.3).

Figure 3.3 Generalised appearance of a completed slide. The sample is retained beneath the coverslip with a wax ring, the mount sealed with Gurr's glyceel and the details recorded on one end.



3.1.5 Enumeration and Identification

All nematodes per sample were counted using a high-power binocular microscope. The 32μM fraction was found to contain <10% of the total number of individuals per sample

and comprised mostly juveniles. Previous deep-sea studies have used >45μm fraction, so the decision was made not to consider the 32μm fraction any further, as part of this study. 100 nematodes were identified from each sample. Numbered slides were selected for identification using a simple random number generator (McAleece, *pers. comm.*) to avoid bias that may have occurred during selection of nematodes for mounting. It had been discovered that larger individuals were subconsciously selected first from the cavity blocks, or left until last. The numbers generated randomly referred to a particular slide number and all individuals on that slide were identified and measured (see below).

Nematodes were identified to genus using a high-power, x100 oil immersion objective, the pictorial key to world genera developed by Platt and Warwick (1983), and also the wider taxonomic literature referenced in the Bremerhaven Checklist of Aquatic Nematodes (1973 and 1974). Due to the very small size of deep-sea nematodes (generally 150-400μm long) and relatively small number of species that have been described from the deep sea, identification to the species level was not possible. Instead, divisions were made within a genus based upon observed morphological differences and then given arbitrary names (sp. A, B, C, etc.).

3.1.6 Biomass and Size Spectra

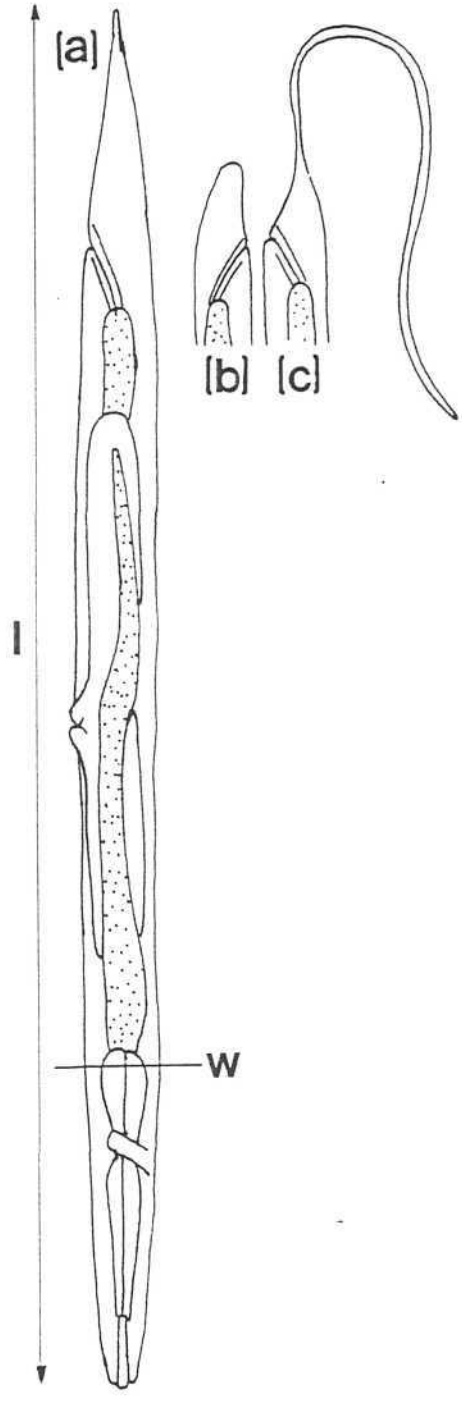
The first 50 individuals that were identified were also measured to determine their volume and dry weight, according to the method of Andrassy (1956). Calculation of volume used the formula:

$$V = \frac{w^2 \times l}{1.7}$$

Where **w** is greatest body width measured at the base of the oesophagus and **l** is body length (Figure 3.4).

As shown in figure 3.4, tail morphology influences the measurement of body length. If the tail forms a regular cone (Figure 3.4a) then the distance from the buccal lips to the tail tip is the body length used in the calculations. However, if the tail is rounded (Figure 3.4b)

Figure 3.4 Diagram indicating where measurements were made on an individual nematode. (a) the generalised tail shape assumed by the volumetric equation, (b) a rounded tail requires extending by eye to form an imaginary cone and measurements are made to this point, (c) measurements are made to the base of a filamentous tail (modified from Andrassy, 1956).



then the tail is extended by eye to form a cone in order to measure body length. Similarly, if the tail is filamentous (Figure 3.4c) then body length is only measured to the base of the filament. Cubic content and weight of the filament are so small as to be considered negligible (Andrassy, 1956).

Measurements of nematode volume were then translated to dry weight by assuming a specific gravity of 1.13 (Wieser, 1960a) and dry weight to be 25% of nematode wet weight (Myers, 1962; Wieser, 1960a), according to the formula of Feller and Warwick (1988):

$$\mathbf{D = \frac{V \times sg \times r}{1{,}000{,}000}}$$

Where **D** is the dry weight (µg), **V** is volume (nl), **sg** is the specific gravity of nematodes (1.13) and **r** is the dry/wet weight ratio (0.25). Although a morphometric method suffers the disadvantages of inaccuracies inherent in conversion factors, it permits preservation of the nematodes for subsequent taxonomic purposes.

Abundance and biomass size spectra were constructed using the X2 geometric size classes of Warwick (1984), where each size class is twice the biomass of the class below (Table 3.2).

Table 3.2 The X2 geometric size classes of Warwick (1984) and the corresponding nematode biomass.

Biomass (µg)	Size Class
19.073 - 38.147	12
9.537 - 19.073	11
4.768 – 9.537	10
2.384 – 4.768	9
1.192 – 2.384	8
0.596 – 1.192	7
0.298 – 0.596	6
0.149 – 0.298	5
0.075 – 0.149	4
0.037 – 0.075	3
0.018 – 0.037	2
0.0931 – 0.018	1
0.0047 – 0.00931	0
0.0023 – 0.0047	-1
0.0011 – 0.0023	-2
0.00058 – 0.0011	-3
0.00029 – 0.00058	-4

3.1.7 Functional Groups

The 100 nematodes that had been identified were also assigned to a feeding group, according to the pictorial classification of Wieser (1953). He distinguished four types: 1A = small/absent buccal cavity with no buccal armature; 1B = moderately-sized buccal cavity with no buccal armature; 2A = moderately-sized buccal cavity with small teeth and 2B = large buccal cavity with large teeth and/or mandibles (Figure 3.5). In addition, the same nematodes were allocated to the tail shape groups of Thistle *et al.* (1995) (Figure 3.6). There are four tail shape groups: rounded with a blunt end, clavate-conicocylindrical (initially conical with extension to the tip), conical (with tail length less than five body widths) and filamentous (with tail length greater than five body widths).

Abundance, biomass, feeding and tail shape groups and identity were recorded from all 0-1 cm samples. In addition, vertical profiles were determined for three replicates from stations at the equator, 5 and 9°N.

Figure 3.5 Feeding types according to Wieser's (1953) pictorial system, taken from Romeyn and Bouwman (1983).

- Type 1A *Selective deposit feeders*
- Type 1B *Non-selective deposit feeders*
- Type 2A *Epistrate feeders*
- Type 2B *Predators/omnivores*

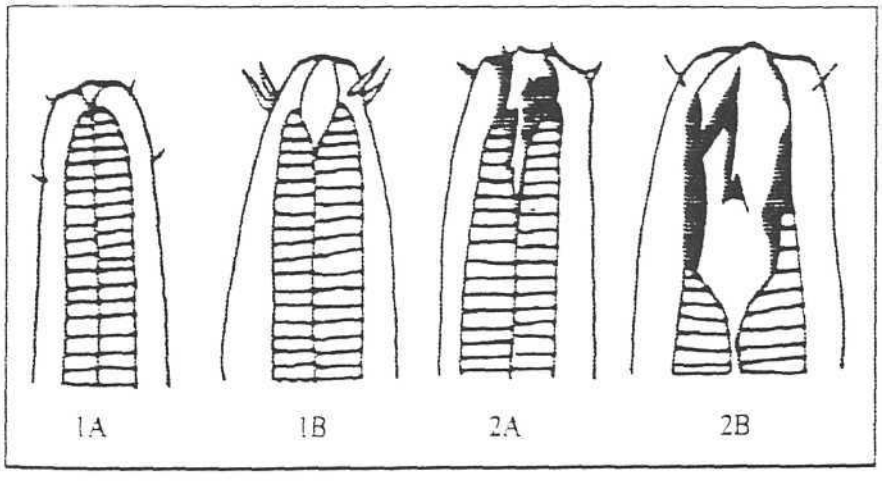


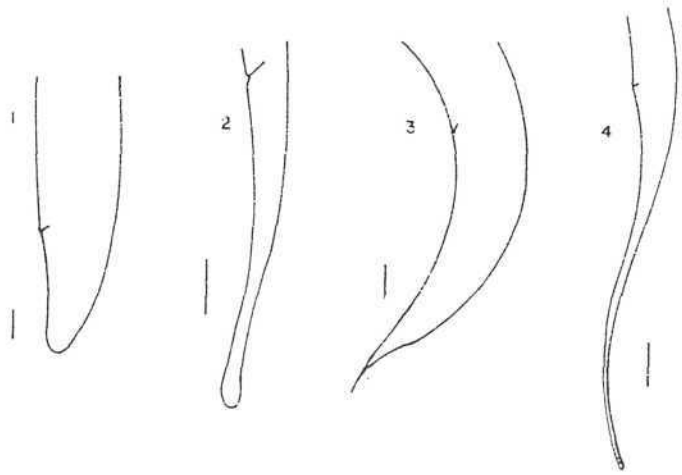
Figure 3.6 Tail shape groups according to Thistle *et al.* (1995). Scale bar represents 10μm.

(1) Rounded with blunt end

(2) Clavate-conicocylindrical

(3) Conical

(4) Filamentous



3.2 Statistical Analysis

The distribution of nematode abundance and biomass at each station was analysed using Minitab for Windows v11.0 statistical package. Due to the discontinuity of the EqPac samples, the assumption of normality is invalid, so consequently, non-parametric tests were used wherever possible. Univariate statistical analyses for α (within-habitat) and β diversity (between-habitat), and multivariate analyses (except NMDS and ANOSIM) were performed using Biodiversity Pro, developed jointly at the Natural History Museum and the Scottish Association for Marine Science. The PRIMER (Plymouth Routines in Multivariate Ecological Research) software package was used for ANOSIM and non-metric multi-dimensional scaling (NMDS) analyses.

3.2.1 Descriptive Statistical Tests

3.2.1.1 The Kruskal-Wallace Test

The *Kruskal-Wallis test* is the non-parametric equivalent of the ANOVA test and tests for differences between the medians of three or more samples. The observations for each sample are ranked as a whole, therefore the test only supplies information for the whole group, as in the ANOVA test. It is safe to assume, however, that if there is a significant difference, it occurs *at least* between the two samples with the highest and lowest sum of ranks (Fowler and Cohen, 1990).

3.2.1.2 The Mann-Whitney U-test

The *Mann-Whitney U-test* is the non-parametric equivalent of the t-test and is used to compare the medians of two independent populations. It is based upon the assumption that the samples exhibit the same *form* of distribution. The test is unaffected by differences in variance, although skewness influences the test to a small degree (Sachs, 1982). It is valid for use with small sample sizes, although with few observations there must be no overlap of observations between two samples for the null hypothesis, H_0, to be rejected.

3.2.1.3 Pearson's Product Moment Correlation Coefficient

Pearson's product moment correlation coefficient, *r*, measures linear correlation (Rees, 1987), and it is a measure of the correlation between all possible pairs of values for each variable. However, it is important to note that a statistically significant correlation does not imply cause and effect, and may instead reflect some underlying factor that is affecting both variables.

3.2.1.4 Row-by-column Test of Independence

This test is used to test the frequency distributions of more than two criteria. The observed frequency distribution is compared with expected frequencies of a hypothetical population in which the frequencies of various classes represent certain proportions of the total frequency. The *G-test* is used to asses goodness-of-fit of the observed distribution to the expected distribution. The test statistic, G, is subsequently compared with the appropriate χ^2 value. The test can be extended to involve tables of three or more dimensions, based upon a log linear model (Sokal and Rohlf, 1969) that tests for the presence of interactions.

Fitting two models, one with the variable present and one with the variable omitted, tests for the effects of a particular variable. The G-statistic is computed for each of the two models and the difference between the G-values used to test the significance of the variable being omitted.

3.2.2 Univariate Analyses

3.2.2.1 The Shannon-Wiener Diversity Index (H')

The *Shannon-Wiener diversity index* is one of many mathematical models used to describe assemblages of organisms in terms of the two components of diversity, species number, and the distribution of individuals between species - the evenness (see review in Heip *et al.*, 1988).

The Shannon Diversity Index, commonly shown as H', has a lower limit of zero when all individuals are of one species, has no upper limit and its behaviour is rather sample-size dependent. As a measure of diversity, H' tends to attribute greater importance to the evenness component (Lambshead *et al.*, 1983). The use of H' must thus be regarded as an indicator of trends rather than absolute values and it is important that its distribution is viewed in conjunction with measures of species richness and evenness. The decision was made to use this index regardless of these problems, because it has been used extensively in prior taxonomic studies and, therefore, offers a means of comparison between studies.

3.2.2.2 Evenness (J')

The *evenness,* or *equitability,* of a sample describes how individuals are distributed between the component species and is inversely related to dominance. A measure of evenness, J', can be calculated using H' as a measure of the ratio of the observed diversity to the theoretical maximum, H_{max}, which would be achieved if all species were equally abundant (Clarke and Warwick, 1994). However, because the number of species in the sample is included in the calculation, the index is highly dependent upon sample size. It is also very sensitive to the chance inclusion/exclusion of rare species in the sample (Heip *et al.*, 1988).

3.2.2.3 Species Richness

This is a measure of the total number of species present as obviously a sample containing more species than another would be considered to be more diverse. It is often given simply as the total number of species, S but this is very sample-size dependent. More commonly *Margalef's Index, d,* is used which incorporates the total number of individuals. Consequently, it provides a measure of the total number of species present for a given number of individuals.

3.2.2.4 Caswell's Neutral Model

Caswell's *neutral model* (1976) attempts to eliminate all forces which might play a role in structuring the observed pattern of species abundance, such as interspecific biotic interactions or differential response to the environment (Platt and Lambshead, 1985). The model generates an ecologically 'neutral' community with the same numbers of species and individuals as the observed community, and determines the theoretical diversity (E(H')) which is then compared with the observed diversity (H'). The deviation statistic, V, is calculated by subtracting E(H') from H' and dividing by the standard deviation of E(H'). When $V = 0$, the sample is said to have been derived from a neutral assemblage. When V is greater or less than zero, the assemblage is not neutral; positive values result from excess equitability, negative values from excess dominance. However, it is worth noting that deviations of H' away from neutral model predictions depend only on differences in equitability as the species richness is fixed (Clarke and Warwick, 1994). The equitability component of diversity may behave differently to species richness in response to stress.

3.2.3 Rarefaction

An obvious index of species richness is the number of species in the sample. However, this method is, of course, highly correlated with sample size. The rarefaction model (Hurlbert, 1971; Simberloff, 1972) predicts the expected number of species for a given abundance of individuals. Rarefaction curves provide a measure of species diversity which permit comparison of α diversity between communities where sample sizes vary. A steeper curve is representative of higher diversity. If the rarefaction curves cross, diversity

of these samples cannot be compared as their relative diversity is highly dependent upon where upon the curves diversity is compared.

3.2.4 Graphical/Distributional Analyses

3.2.4.1 *k*-dominance Curves

Shaw *et al.* (1983) suggested that ranked species abundance curves were a sensitive means of detecting differences in dominance patterns. Where no species shows overwhelming dominance it is necessary to consider the combined dominance of the *k* most abundant species. An assemblage can be considered to exhibit more dominance than a second assemblage if, for all possible values of *k*, the *k*-dominance of the first assemblage is greater than or equal to the *k*-dominance of the second. As dominance is the opposite of equitability and is similarly inversely related to diversity, then one assemblage is more diverse than a second if, for all values of *k*, the *k*-dominance is less than or equal to that of the second. The *k*- dominance curve is obtained by plotting *k*-dominance as percentage cumulative abundance against *k* (species rank). Thus, assemblage A is considered to be more diverse than assemblage B if the *k*-dominance curve for assemblage A is always below or touching the *k*-dominance curve for assemblage B. However, if the two curves intersect, then the assemblages cannot be compared in terms of intrinsic diversity. In these cases, indices of diversity cannot be relied upon to give the same diversity ordering; the diversity index used may determine which assemblage is deemed to be the most diverse (Lambshead *et al.*, 1983).

3.2.4.2 Species Richness Estimators

The simplest species richness estimator plots cumulative species richness against a cumulative number of new species by random addition of each sample. This provides a species richness value that is more representative of the species pool than provided by individual sample observations. The slope of the species richness curve can be used to indicate differences in species turnover, a measure of β (between-habitat) diversity (He and Legendre, 1996). Species richness curves were plotted using BioDiversity Pro, which performs five random sorts when pooling the samples. A steeper curve is representative of higher regional diversity.

3.2.5 Multivariate Statistical Analyses

Taxonomic or functional identities are not retained during univariate analyses and, consequently, these methods might indicate the occurrence of similar community structures in samples that have an entirely different suite of species. Similarly, communities that appear to be entirely different using univariate methods of analyses could have a similar or identical species composition. Multivariate analyses of community structure retain the identity of each species or functional grouping (such as nematode feeding type) and therefore provide information on the different structural properties of species assemblages.

Most multivariate techniques rely upon measures of the similarity of species abundance between pairs of samples. A similarity matrix can be used to discriminate sites from each other (e.g. ANOSIM test), cluster sites into groups that have similar communities (e.g. cluster analysis), or allow a graphic representation of a graduated ordination of sites (e.g. Principal Components Analysis, Correspondence Analysis).

A number of similarity coefficients have been suggested in the past, but the one that has been used most frequently is the Bray-Curtis coefficient of similarity (also known as the Czekanowski coefficient) (Clarke and Warwick, 1994). It has been used quite successfully on nematode species abundance by a number of researchers (Tietjen, 1976; Tietjen, 1977; Tietjen, 1984; Austen and Warwick, 1989; Tietjen, 1989; Austen *et al.*, in press). Sample dissimilarity is the converse of sample similarity and is simply the degree to which two samples are unlike each other. It is a particularly useful starting point in ordinations (e.g. NMDS – see later), where dissimilarities are turned into distances between sample locations on an ordination map. Large dissimilarity values imply that the samples be located at a large distance from one another on the map and dissimilarities near zero imply nearby location. The distance between two sample locations on the map can be measured geometrically and is termed *Euclidean* distance (Clarke and Warwick, 1994).

Similarities or dissimilarities between samples are often heavily dominated by counts for the most abundant species. This can be overcome be transforming the data so that all species contribute something to the definition of similarity/dissimilarity. Again, a number

of transformations have been developed, but the method used in this study is the *double root* (or *4th root) transform*. This affects the data such that the importance of the very abundant species is severely down-weighted, and increases the role of the less common and rare species in determining similarity/dissimilarity is increased. It has been recommended for use on biological data on community structure such as this (Clarke and Warwick, 1994) and more specifically, on nematodes (Hodda, 1986).

3.2.5.1 ANOSIM

The ANOSIM (analysis of similarity) randomisation test (Clarke and Green, 1988) is used to confirm differences between groups of sites with similar species assemblages. ANOSIM is a conservative test that determines if samples, which appear to be grouped in separate clusters, really do form distinct groups. A test statistic is calculated, based upon the difference in average rank dissimilarities between and within groups. Samples are subsequently repeatedly, randomly, reallocated to different groups and the test statistic re-computed. ANOSIM then determines whether the test statistic derived from the original groupings is significantly different from those derived from the random groupings (Clarke and Warwick, 1994). The basic design is extended to consider a two-way nested experimental design, where two levels of spatial replication are involved e.g. sites are grouped *a priori* to be representative of two "treatment" categories (with phytodetritus and without) but there are also replicate samples taken within that site.

3.2.5.2 Cluster Analysis

Cluster analysis (or *classification*) aims to place samples in groups so that the samples within a group are more similar to each other than samples in different groups. It is used in this study to determine whether different sites have a distinct community composition, by noting that replicate samples from the same site fall within a cluster that is distinct from replicates within other sites. This is an important consideration because if replicates for a site are clustered more or less randomly with those from other sites then further interpretation or analysis would be uninformative.

There are a number of clustering methods available but the one used in this study is the *hierarchical agglomerative method* (Cormack, 1971). This method uses a similarity matrix to sort the samples into groups and then the groups into clusters, beginning with the

highest similarities, then lowering the similarity level as the groups are formed. The process ends with all groups contained in one cluster. The results are subsequently displayed as a hierarchical tree or *dendrogram,* where the *y*-axis represents the similarity level at which the two samples are considered to have joined and the *x*-axis the full list of samples (Clarke and Warwick, 1994).

This clustering method is prone to a number of problems that must be observed when interpreting the data. Cluster analysis attempts to group samples into discrete clusters and thus does not provide information on inter-relationships on a continuous scale. The resulting order of the samples along the *x*-axis is not unique and thus to use the sequence of samples on the *x*-axis as an ordering is incorrect. Also, the hierarchical nature of this clustering process means that once a sample is grouped with others, it will not be separated from them at later stages in the process. Consequently, early borderline decisions are perpetuated through the process and may have a significant effect on the final arrangement of the dendrogram. Finally, clustering is less useful where there is a steady change in community structure e.g. along an environmental gradient and can be misleading. Ordination methods such as NMDS are preferable in these situations.

3.2.5.3 Non-metric Multi-dimensional Scaling (NMDS)

Ordination methods provide a map of the samples, usually in two dimensions, where the placing of the samples can be related to the dissimilarity of their species communities i.e. points close to one another have very similar communities and samples which are far apart have few species, or the abundance of those species, in common. As with clustering there are a number of methods but the one chosen for this study is *non-metric multi-dimensional scaling* (NMDS).

The main weakness of clustering methods, as already identified, is their inflexibility of dissimilarity measure. Originally developed for use in psychology studies (Kruskal, 1964), NMDS is based upon relative values of similarity i.e. how much sample 1 is similar to sample 2 compared with sample 3. The analysis begins with a similarity or dissimilarity matrix between samples and in this study the Bray-Curtis index of dissimilarity was used with and without double-root transformation. Dissimilarity measures are projected in low-

dimensional ordination space to make a "map" of the samples that attempts to preserve conditions imposed by the rank dissimilarity matrix (Clarke, 1993).

The NMDS algorithm is an iterative procedure that constructs the NMDS plot by successively refining the positions of the points until they satisfy the dissimilarity relationships between samples. A number of steps are followed during the procedure. Firstly, the number of ordinations must be specified (2 in this study) for the final ordination plot. The samples are then placed in a starting configuration which is simply a random set of points in two dimensional space, and the inter-point distances from this plot are regressed on the corresponding dissimilarities. A non-parametric regression is performed on a scatter plot of distance against dissimilarity. This is a line of best fit that molds itself to the shape of the scatter plot, but is constrained to always increase. This is what gives NMDS its greater flexibility than other ordination methods. The extent to which the scatter points deviate from this line measures the failure to match the rank order dissimilarities and is called the "stress" value. Large scatter clearly leads to large stress and can be thought of as measuring the difficulty in compressing sample relationships into two dimensions. The current configuration is then perturbed in the direction of least stress, based upon the method of "steepest descent" (Clarke and Warwick, 1994). Simply put, the regression relation is used to evaluate the stress for small changes in the position of point in the ordination and points are then moved in directions that predict the most rapid decrease in stress. The iteration now cycles around the two stages of regression of distance on similarity for the new ordination positions followed by further perturbations in the direction of decreasing stress. The cycle stops when further perturbations cause no reduction in stress.

The stress value can provide a measure of the adequacy of the NMDS representation. Although stress increases with reduced dimensionality and increased quantities of data, there are rough guidelines for particular stress levels (Clarke, 1993): stress < 0.05 gives an excellent representation of the data with no prospect of mis-interpretation; stress < 0.1 corresponds to a good ordination, with little risk of making false inferences; stress < 0.2 can still produce a useable picture, although for values close to 0.2 there is potential for misinterpretation, but a higher dimensional solution could show a different picture. Stress > 0.2 is likely to yield plots that may be dangerous to interpret. Field *et al.* (1982)

suggested that conclusions could be cross-checked against those made from an alternative ordination. The superimposition of cluster groups chosen at a spread of arbitrary hierarchical levels should not distort the ordination plot. Greater than 0.35 the points are effectively randomly placed, bearing little relation to the similarity ranks.

One potential problem with the algorithm is that convergence in the iterative procedure may occur at a local minimum, where no further reduction in stress can be achieved for the current configuration, but a different configuration may have an even lower stress. This is easily overcome by repeating the analysis several times until similar lowest stress value ordinations are achieved. If the data are clearly divided into two groups then a second problem may arise. If the two groups have no species in common then there is no yardstick for determining how far apart the groups should be placed in the NMDS plot. They are, in fact, infinitely far apart and consequently the samples in each group collapse to a point. The solution in this instance is to split the data into two groups and carry out separate ordinations on each group.

NMDS has been recommended as one of the best ordination techniques available (Kenkel and Orloci, 1986; Clarke, 1993; Clarke and Warwick, 1994). It is better able to represent complex relations more accurately in low-dimensional space than other ordination methods or cluster analysis, and is generally applicable, particularly where there are no clear groupings or one strong gradient of change across all groups. It is based upon a simple concept and fewer assumptions are made about the nature and quantity of the data than with any other ordination method, making it a very flexible analytical tool.

4.1 Introduction

Twenty years ago the benthic communities over vast expanses of the abyssal sea-floor were thought to be a severely food-limited; the organic carbon content of central ocean sediments could be as little as 0.1% (Gage and Tyler, 1991). The predominant view of organic-carbon export flux from the surface water was one of a steady, sparse rain of mostly refractory organic material known as marine snow (e.g. Riley *et al.*, 1964). Consequently, benthic standing-stocks were presumed to be among the lowest recorded anywhere in the marine environment. However, as discussed in chapter 1, close links between the surface ocean and its underlying seafloor are now well established (see review in Graf, 1992). In areas where phytoplankton blooms occur, a portion of the material produced sinks so rapidly through the water column, that it is deposited at the sea floor, thousands of metres below, in only a few weeks (Deuser *et al.*, 1981; Lampitt, 1985; Asper, 1987; Deuser *et al.*, 1990; Honjo and Manganini, 1993).

This rapid removal of particulate organic material represents a significant net downward flux of carbon and nitrogen. Estimates from the NE Atlantic, based upon the phytodetritus standing crop on the seafloor, suggest that up to 3% of the spring primary production reaches the seabed at 4,500m (Thiel *et al.*, 1988/89). The presence of measurable quantities of chlorophyll *a* in the phytodetritus suggests that the material arrives relatively undegraded (Billett *et al.*, 1983; Lampitt, 1985) and hence may represent a significant input of organic carbon to the sediments. Consequently, ever since Billet *et al.* (1994) observed the arrival of a seasonal pulse of phytoplankton material at the abyssal seafloor in the NE Atlantic, attempts have been made to assess the impact of this carbon-rich material on the benthos, including the meiofauna.

Studies have been made at several sites that receive varying inputs of phytodetrital material, in this region of the North Atlantic (see reviews in Bett *et al.*, 1994; Vincx *et al.*, 1994). Bacteria and some protists respond to sedimentation of phytodetritus by rapidly colonising the phytodetrital aggregates and showing marked increases in biomass and abundance (Lochte and Turley, 1988; Turley *et al.*, 1988; Pfannkuche, 1992). A fast

reaction, i.e. over a few weeks, of deep-sea Foraminifera in response to the seasonal sedimentation of phytodetritus was recorded at bathyal depths in the Porcupine Seabight (Gooday, 1988; Lochte and Turley, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Pfannkuche, 1992) and from the Arctic shelf break (Pfannkuche and Thiel, 1987). It has been proposed that this rapid response is facilitated by the short generation times of protozoans and possibly by activation of resting stages or dormant cells (Soltwedel *et al.*, 1996).

Nematodes should be able to benefit either directly or indirectly from phytodetrital sedimentation as they feed largely on bacteria, algae and particulate material (Heip *et al.*, 1985; Jensen, 1987; Giere, 1993; Soltwedel and Thiel, 1995). However, conflicting evidence has been reported concerning a nematode response to food availability in the deep sea. Soetaert and Heip (1989) found a positive correlation between chloroplastic pigment equivalent concentrations and mean body size along a transect in the Mediterranean. Similarly, at two stations in the NE Atlantic, Vanreusel *et al.* (1995) and Soltwedel *et al.* (1996) noted a significant increase in mean individual size at the station receiving a greater input of phytodetritus. Lambshead *et al.* (1995) noted that sedimentation of phytodetritus was also correlated to the occurrence of large individuals deeper in the sediments. In his study in the western Pacific, Shirayama (1984a) correlated increases in biomass and abundance to higher surface chlorophyll *a* concentrations. However, in an earlier study, Shirayama (1983) had noted that food availability did not control the size structure of nematode communities. Likewise, Pfannkuche (1992) and Gooday *et al.* (1996) found no evidence that phytodetritus caused significant increases in abundance or biomass or influenced the vertical distribution of nematodes in the sediments.

During the 1992 US JGOFS program in the central equatorial Pacific, abyssal accumulations of phytodetritus were observed along a narrow latitudinal band at 140°W for the first time in the Pacific Ocean (Smith *et al.*, 1996). Between 5°S and 5°N, the presence of measurable quantities of chlorophyll *a* and excess ^{234}Thorium (tracers with degradation time-scales of less than one hundred days, Stephens *et al.*, 1997, and Aller and DeMaster, 1984, respectively), phytoplankton cells with intact chloroplasts and high respiration rates of associated microbial populations implied that this material was

recently settled and relatively undegraded (Smith *et al.*, 1996). In contrast, the surface fluff at 9°N appeared to be much more refractory in nature. Overall, the annual, abyssal, POC flux exhibits a four-fold increase between 9°N and the equator (Dymond and Collier, 1988; Honjo *et al.*, 1995).

In the surface waters of the equatorial Pacific, convergence zones are generated by upwelling within a narrow latitudinal band along the equator (Philander, 1989). Tropical instability waves (TIWs) (Yoder *et al.*, 1994), caused by shear between the westward-flowing South Equatorial Current and the eastward North Equatorial Counter Current (Archer *et al.*, 1997), propagate westwards along the equator between 90° and 160°W and oscillate between 2°S and 5°N (Flament *et al.*, 1996). Buoyant diatom species such as *Rhizosolenia* (Yoder *et al.*, 1994) are concentrated by the passage of TIW's and Smith *et al.* (1996) proposed that these intense diatom patches flocculate and form dense phytodetrital aggregates that settle rapidly to the seafloor. This explains, in part, the observed occurrence of phytodetritus from the equator to 5°N.

Bottom photographs demonstrated the importance of phytodetritus to deep-sea detritivores. Feeding gaps and grooves that exposed the underlying white carbonate sediments suggested active removal by grazing echinoids, echiurans and holothurians. The abundance of mobile megafauna was an order of magnitude greater at the equator than it was at 9° (Smith *et al.*, 1997). Additionally, megafaunal burrows were found to be preferentially enriched with phytodetrital material at depths of 17-27cm in the sediments at the equator. Smith *et al.* (1993) hypothesised that this demonstrated active selection for organic-rich material by animals, such as echiurans (Hoover *et al.*, 1994; Smith, 1994), responsible for caching the phytodetrital material.

Glutamate-uptake and respiration measurements indicated that the phytodetrital material harbours an especially active microbial population; measured respiration rates were five times greater than in underlying sediments (Smith *et al.*, 1996). This suggests that the phytodetritus is rich in labile algal compounds and, correspondingly, microbial biomass (Smith *et al.*, 1996). All of these factors imply that phytodetritus was a relatively rich food resource utilisable by deep-sea nematodes and consequently might affect population distribution within the sediment.

The abundance and biomass of nematodes of the equatorial Pacific were used to test the following hypotheses:

- Elevated particulate organic carbon (POC) flux is not correlated with a significant increase in nematode abundance or biomass in the abyssal, equatorial Pacific

- Bioturbation effects by larger organisms are not correlated with the vertical distribution of nematodes

- Elevated POC flux is not correlated with an increase in mean body size in EqPac nematodes

4.2 Results

4.2.1 Horizontal Distribution of Abundance and Biomass

At each station, abundance within individual cores varied quite markedly and was particularly low in sample BC4 (equator) and particularly high in sample BC22 (9°N) (Table 4.1). Study of the cruise log (Smith *pers. comm.*) indicates that the BC4 box-core had slightly turbid surface water suggesting that the surface sediments had been disturbed. Box-core BC22 was in excellent condition on arrival shipboard but box-cores BC19 and BC20 (also from 9°N) showed some indication of sediment disturbance, and appeared to have entered the sediments at a slight angle. It is possible, therefore, that BC4 could be considered as not 100% intact and likewise for samples BC19 and BC20. However, the distribution of nematodes is known to be very patchy (Hogue, 1982; Thistle and Sherman, 1985) and the discrepancies may simply reflect this. Consequently, the decision was made not to apply any correction factor to the data observed from these cores.

When 0-5°N and 9-23°N station values were combined into two groups, both abundance and total biomass were significantly different ($P = 0.0109$ using a Mann-Whitney Confidence Test). The decision to group the stations in this manner corresponds to the occurrence of phytodetritus overlying sediments and also greater POC flux measured into deep-moored sediment traps. Nematode abundance in the top centimetre increased by 50% between the equatorial station and that at 2°N (Table 4.1). Subsequently it decreased with increasing latitude to a minimum value of 40.3 ± 9.17 individuals per 10 cm^2 at 23°N (Figure 4.1). As a consequence of the high intra-station variability and small number of cores taken at some stations, these changes were not statistically significant (type I error).

A comparative study made by Bett *et al.* (1994) that indicated that approximately 40% of nematodes were lost from box-core samples due to the bow-wave effect of the sampling gear. In the present study, box core samples were used in addition to multiple core samples. A correction factor of 0.4 was applied to the box-core nematode abundance values (Figure 4.2) to determine whether use of both sample types in the same tests was valid. Bett *et al.* (1994) noted that box-corer effects varied according to type of box-corer, sediment type and the presence or absence of phytodetritus and it was concluded that, in

Table 4.1 Surface (0-1cm) abundance, A (ind./10cm2), total biomass, B (µg/100cm²) and individual biomass, I (ug) for each core with Kruskal-Wallis test statistic, Z

	0°			2° N			5°N			9°N			23°N		
	A	B	I	A	B	I	A	B	I	A	B	I	A	B	I
	8.6	9.982	0.116	76.3	19.920	0.026	63.7	183.943	0.289	20	10.246	0.051	45.625	11.699	0.026
	102.2	48.758	0.048	89.6	150.497	0.168	72.6	20.948	0.029	25.8	8.734	0.034	28.125	8.352	0.030
	21.1	4.115	0.020	59.6	81.251	0.136	71.8	109.889	0.153	88	37.706	0.043	38.75	43.002	0.111
	91.5	27.060	0.030	159.8	77.716	0.049	54.3	12.952	0.024				48.875	14.519	0.030
	74.8	63.850	0.085				59.875	109.066	0.182						
Mean	59.6	30.753	0.055	96.325	82.346	0.095	64.455	87.360	0.127	44.6	18.895	0.043	40.343	19.393	0.049
St Dev	42.26	25.369	0.212	44.061	53.430	0.643	7.826	71.158	0.831	37.697	16.308	0.071	9.174	15.940	0.112
1 S.E.	18.9	11.345	0.013	22.03	26.715	0.045	3.5	31.823	0.052	18.849	9.416	0.006	5.297	7.970	0.008
Z	0.250	-0.830	-0.580	1.880	1.610	0.720	0.330	1.650	0.910	-1.01	-1.310	-0.100	-1.61	-1.340	-0.990

Abundance $P = 0.202$
Total Biomass $P = 0.106$
Individual Biomass $P = 0.718$

Figure 4.1 Surface (0-1cm) mean nematode abundance along the JGOFS EqPac 140°W transect. Error bars are ± 1s.e. Note that the × - axis is not to scale.

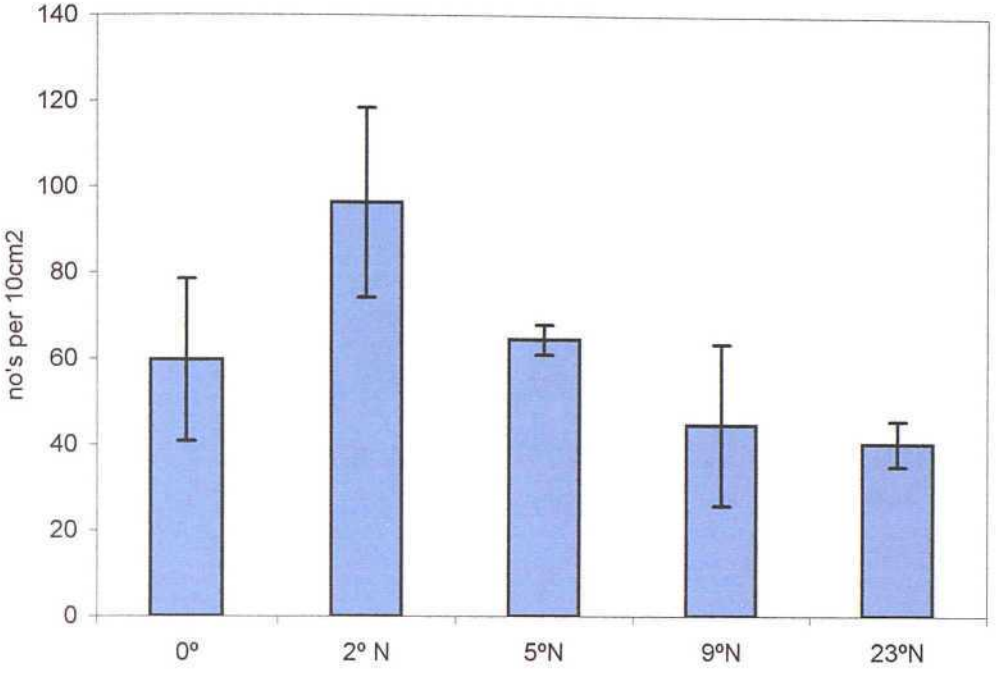
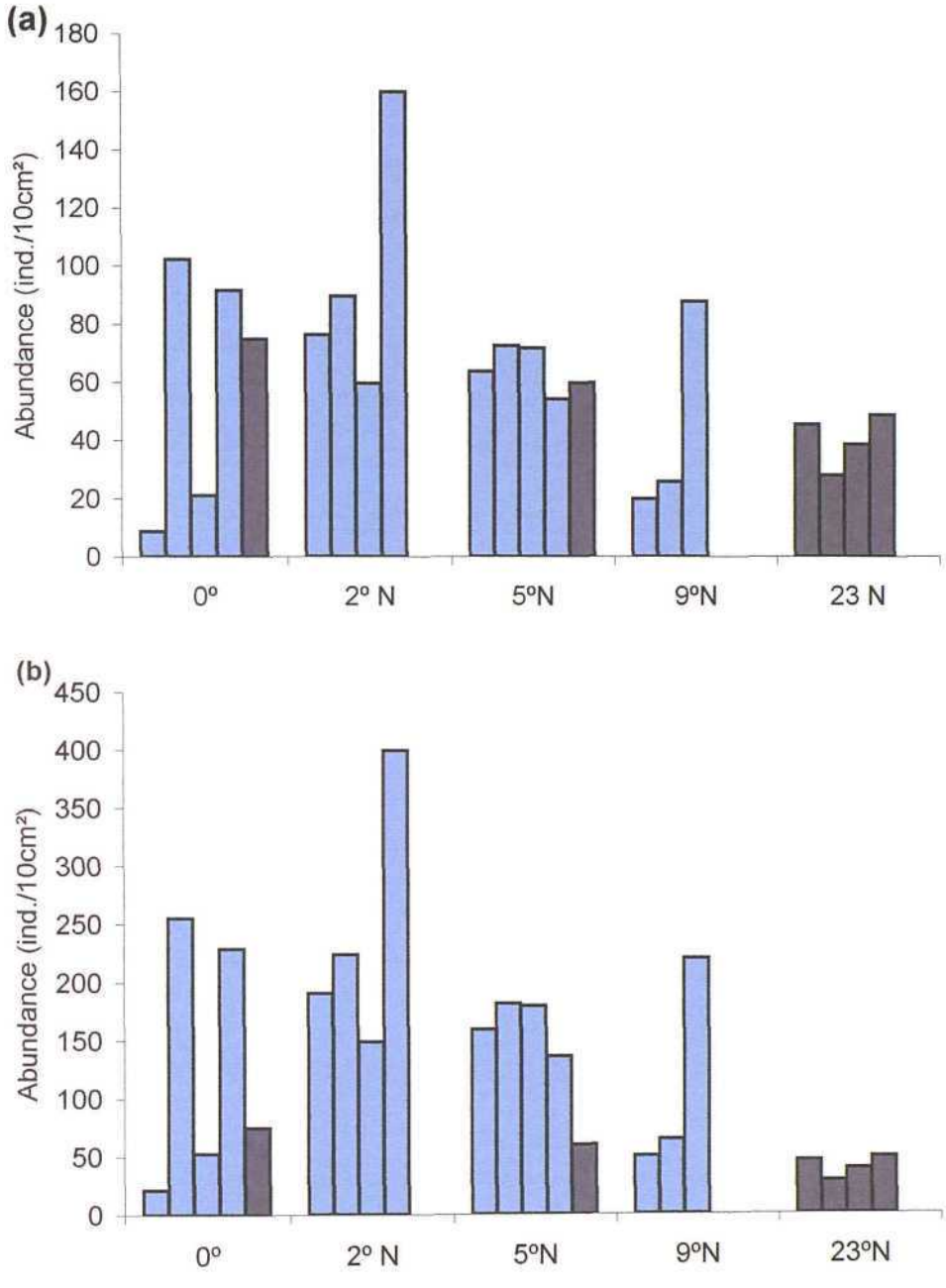


Figure 4.2 Surface (0-1cm) abundance for individual cores along the 140°W transect. (a) uncorrected data and (b) data after correction factor has been applied to the box-core samples. Multiple-core samples are shown in purple. Note that the × - axis is not to scale.



this study, the box-corer did not appear to sample the EqPac nematodes less quantitatively than the multiple-corer. All samples from a particular station were therefore treated as replicates, regardless of collection method, as adopted in other studies (e.g. Boucher and Lambshead, 1995; Thistle *et al.*, 1995).

When compared with all other stations (Figure 4.3), biomass in the top centimetre was highest at 5°N, but again the difference was not significant (Table 4.1). Additionally, biomass did not decrease at higher latitudes (19.39 ± 7.97µg) to values significantly lower than at the equatorial station (30.75 ± 11.345µg). Mean individual biomass was also greatest at 5°N (Table 4.1, Figure 4.4). Stations at 9° and 23°N demonstrated similar grouping for mean individual biomass as total biomass and abundance, but neither were significantly different from stations at lower latitudes. In addition, when individual biomass was combined for stations 0-5° and 9-23°N, there was no significant difference (P = 0.0663 using a Mann-Whitney Confidence Test). Table 4.2 contains whole-core data for abundance, biomass and mean individual biomass. A Kruskal-Wallis test indicated no significant difference in any variable between any stations (Table 4.2).

The most noteworthy observation of changes with latitude was that maximum density and biomass did not occur at the same location (2° and 5°N respectively). This is demonstrated in figure 4.5 where abundance plotted against biomass suggests that a trend for increasing numbers of slightly larger individuals with latitude is abruptly interrupted at 5°N by reduced numbers of much larger individuals.

4.2.2 Vertical distribution of abundance and biomass within the sediments

The distribution of nematodes within the upper 5cm of sediment was remarkably similar for all three JGOFS EqPac stations (Figure 4.6, Table 4.3). This similarity was confirmed by the distribution of proportional abundance. In all three cases approximately half of the total number of nematodes occupied the top 1cm and one quarter of the total number occurred in the 1-2cm sediment layer. However, variability was markedly higher in the 0-1cm layer at the equator and 9°N. Below the 2cm horizon, abundance appeared to remain relatively constant and at an almost identical value for the equatorial and 5°N stations (15.0 ± 3.383 ind.10 cm^{-2}). At 9°N there was a sub-surface increase in numbers in the 3-

Figure 4.3 Mean total surface (0-1cm) biomass along the JGOFS EqPac 140°W transect. Error bars are ± 1s.e. Note that the × - axis is not to scale.

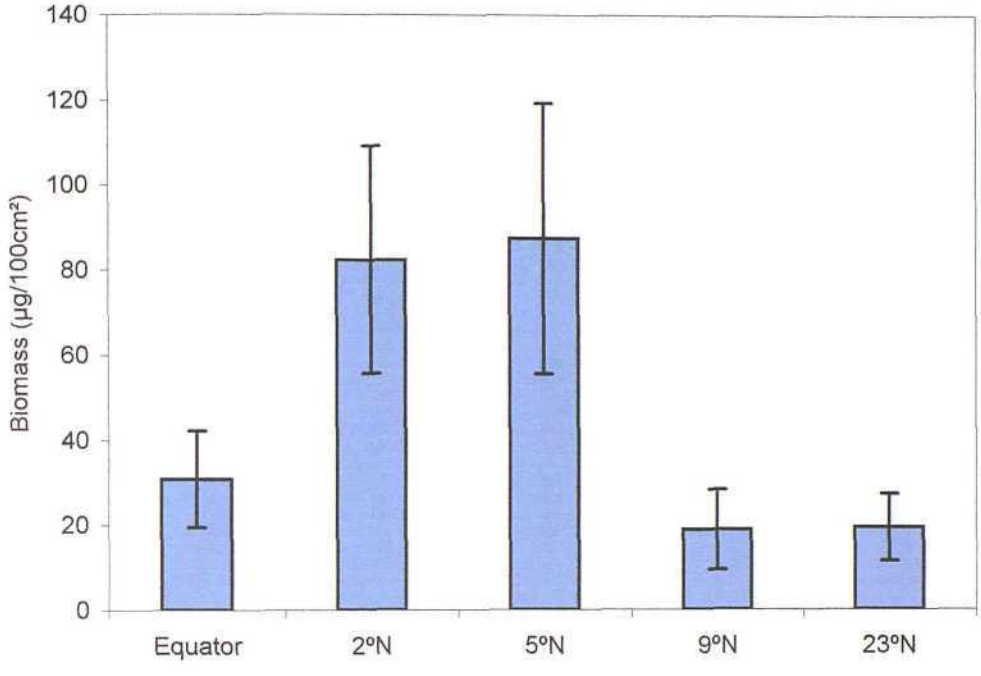


Figure 4.4 Surface (0-1cm) mean individual biomass along the JGOFS EqPac 140°W transect. Error bars are ± 1s.e. Note that the × - axis is not to scale.

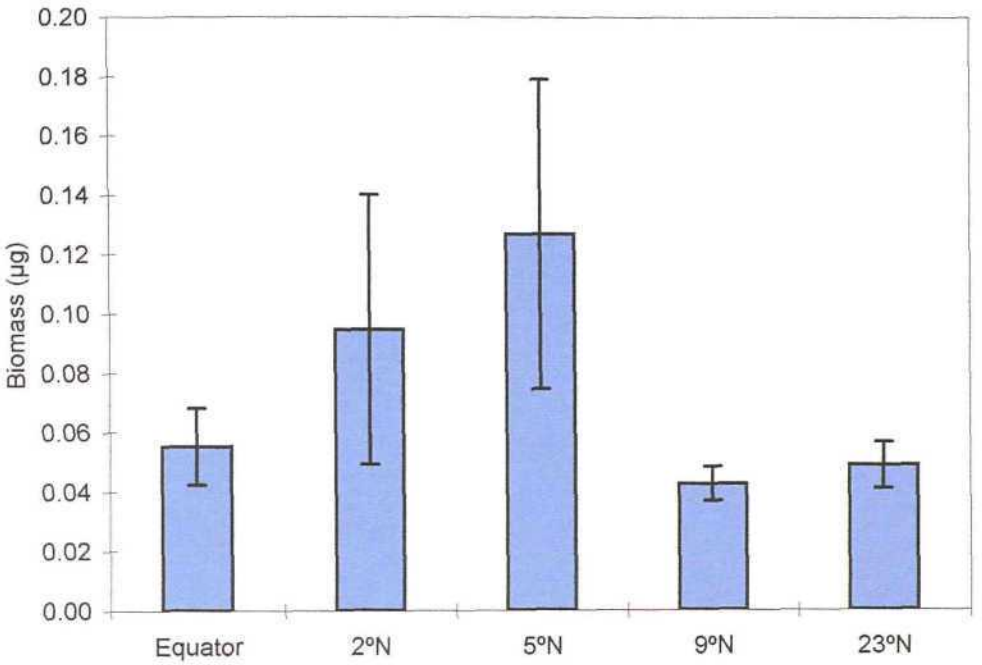


Table 4.2 Mean whole-core (0-5cm) abundance, A, total biomass (μg), B, and individual biomass (μg), I, with Kruskal-Wallis test statistic, Z.

	0°			5°N			9°N		
	A	B	I	A	B	I	A	B	I
	496	20.909	0.0473	1506	234.808	0.1074	657	27.552	0.0380
	1857	136.498	0.0829	1096	32.726	0.0302	546	23.787	0.0324
	1656	51.889	0.0340	1479	136.044	0.0629	1509	62.744	0.0392
Mean	1336.333	69.765	0.055	1360.333	134.526	0.068	904.000	38.028	0.046
St Dev	734.657	59.832	0.194	229.317	101.050	0.521	526.877	21.488	0.183
1 S.E.	424.154	34.544	0.008	132.396	58.341	0.021	304.192	12.406	0.007
Z	0.77	-0.26	0.020	0.000	1.290	0.340	-0.77	-1.030	-0.350

Abundance $P = 0.670$
Total Biomass $P = 0.393$
Individual Biomass $P = 0.924$

Figure 4.5 Nematode abundance vs. mean individual biomass for all stations. Error bars are ± 1s.e.

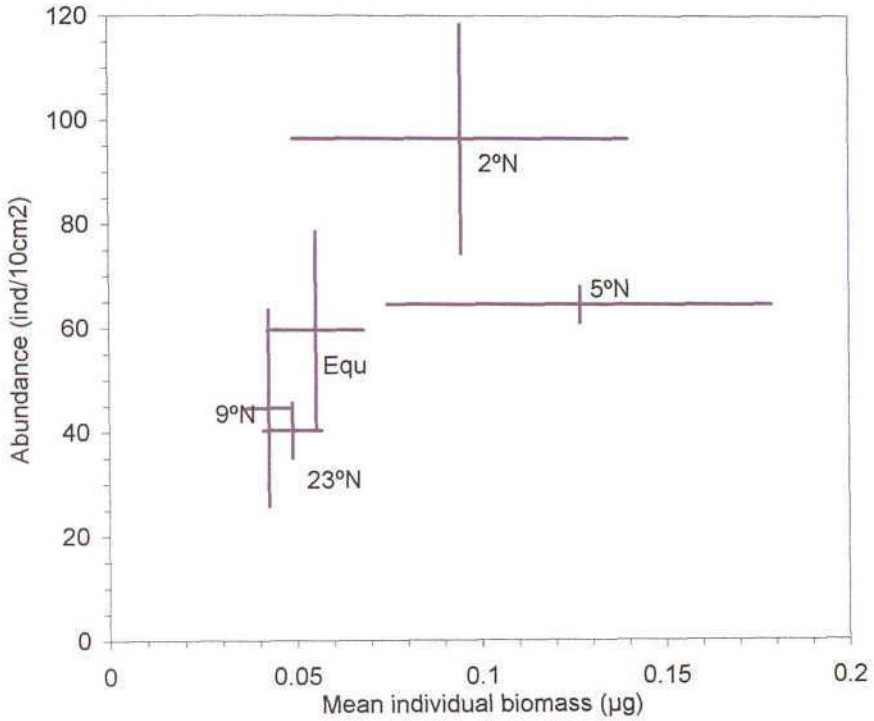


Figure 4.6 Vertical distribution of mean nematode abundance with sediment depth for three JGOFS EqPac stations: (a) absolute and (b) proportional abundance. Error bars are ± 1s.e. Note that 3-5cm sediment layer represents a 2cm layer.

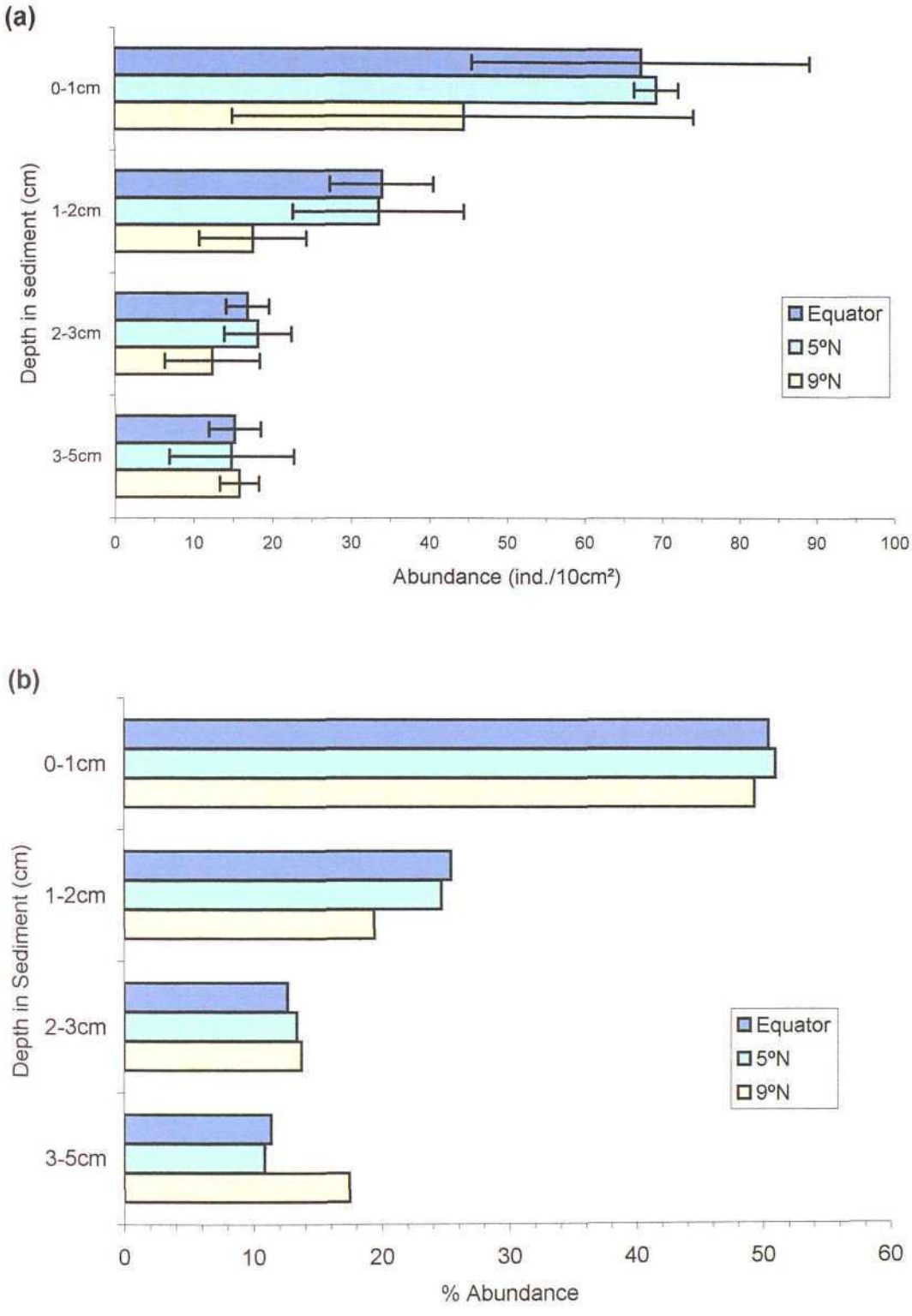


Table 4.3 Mean abundance (ind/10cm²), A, total biomass (μg/100cm²), B and individual biomass (μg),I, per depth interval (± 1s.e.) for each station

	0°			5°N			9°N		
	A	B	I	A	B	I	A	B	I
0-1cm	67.43±51.23	28.60±11.220	0.036±0.005	69.37±4.92	04.927±47.11	0.157±0.085	44.6±37.70	18.895±9.416	0.043±0.006
1-2cm	34.03±11.79	27.985±17.21	0.081±0.027	33.6±18.89	20.365±7.873	0.058±0.011	17.57±11.41	10.729±1.921	0.082±0.029
2-3cm	16.93±10.43	6.045±2.710	0.033±0.004	18.23±7.39	6.133±3.641	0.030±0.009	12.43±4.72	3.310±0.200	0.029±0.004
3-5cm	15.23±4.34	7.135±3.864	0.041±0.015	14.83±13.68	3.101±0.312	0.032±0.007	15.8±5.7	5.093±1.504	0.031±0.006

5cm sediment layer although this increase was not significant. This increase corresponded to proportionally fewer individuals in the 1-2cm sediment layer compared with the other two stations.

Nematode biomass was distributed differently to density within the sediments (Table 4.3). Considering total biomass first, different patterns of distribution were found for each station. The distribution of biomass at 5°N (Figure 4.7) closely matched that of abundance. Three-quarters of the total biomass occurred in the 0-1cm layer, dropping markedly to only 15% of the total in the 1-2cm layer. Below the 2cm horizon, total biomass continued to decrease exponentially. At 9°N, the distribution of biomass also corresponded to the distribution of numbers with proportionally less biomass distributed in the upper 2cm and a sub-surface peak in the 3-5cm layer. At the equator approximately 80% of the total biomass was found in the upper 2cm, distributed evenly. There was a faint suggestion of a sub-surface peak in the 3-5cm layer.

The marked peak in biomass in the 0-1cm layer at 5°N was significantly greater than the biomass of the other two stations. Some of this peak can be attributed to a single, large predator/scavenger nematode (*Mesacanthion* sp.) that accounted for a high proportion of the total 0-1cm sample biomass. Removing this individual from the data set reduced the mean measured biomass from 7.844 ± 6.5µg to 3.835 ± 3.341µg (a drop in mean total biomass from 104.927 ± 47.12µg.100cm^{-2} to 48.809 ± 42.564µg.100cm^{-2}). The decision was made to leave this individual in the data set as it was felt that (1) the fifty individuals used for biomass measurement had been chosen randomly and thus were considered to be representative of the sample population and (2) as a predator/scavenger type, this individual may feed directly on the phytodetritus in addition to other nematodes (Jensen, 1987) and hence may well be a significant consumer of organic carbon within the population.

The distribution of mean individual biomass appeared to be different again (Figure 4.8). A pronounced sub-surface peak in individual biomass occurred in the 1-2cm sediment layer at both the equator and at 9°N. This represented a significant increase in body size from that in the 0-1cm layer and also in the 2-3cm layer. Individual biomass above and below this sediment layer was similar at all depths for both stations. At 5°N maximum individual

Figure 4.7 Vertical distribution of mean total biomass with sediment depth for three JGOFS EqPac stations: (a) absolute and (b) proportional biomass. Error bars are ± 1s.e. Note that 3-5cm sediment layer represents a 2cm layer.

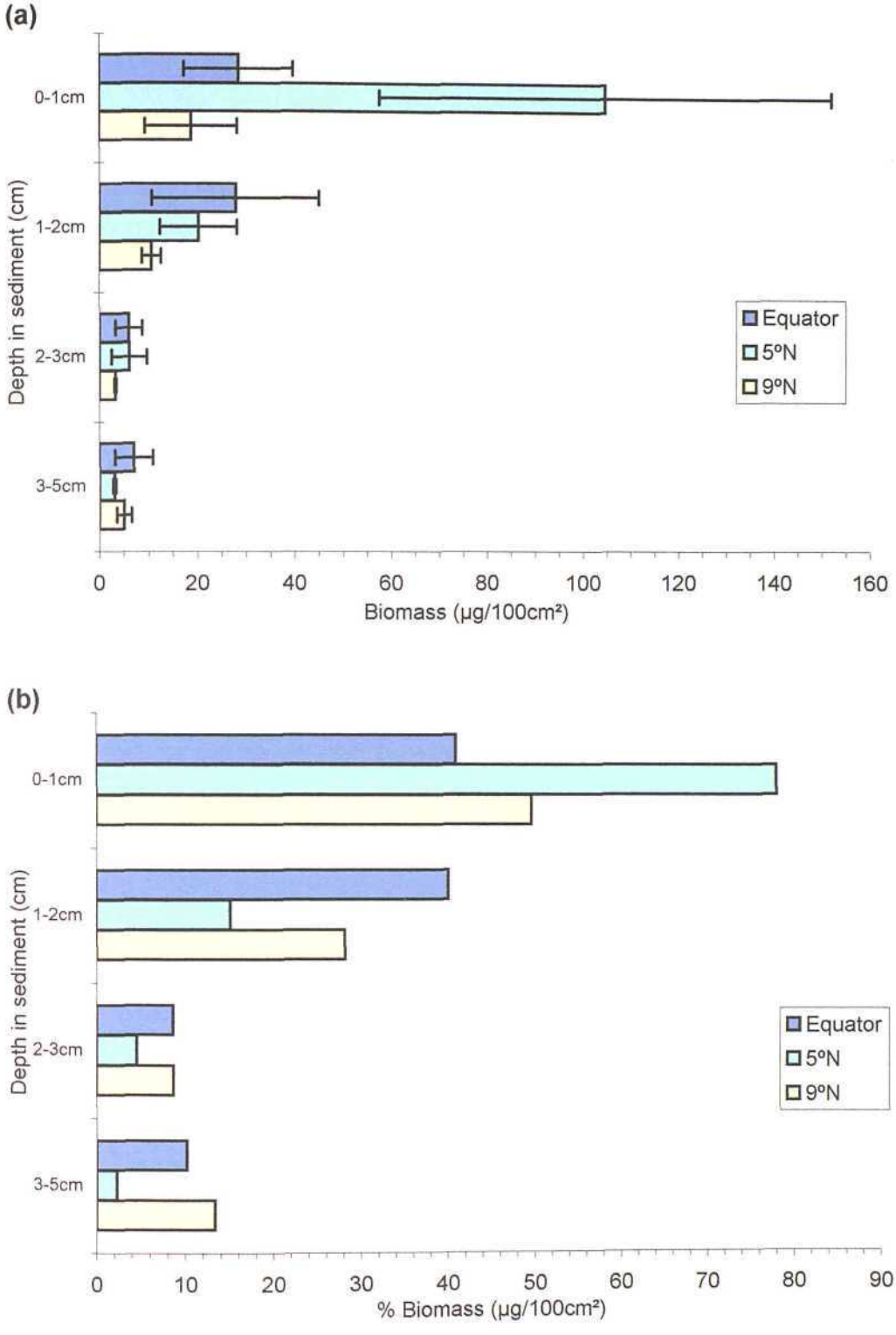
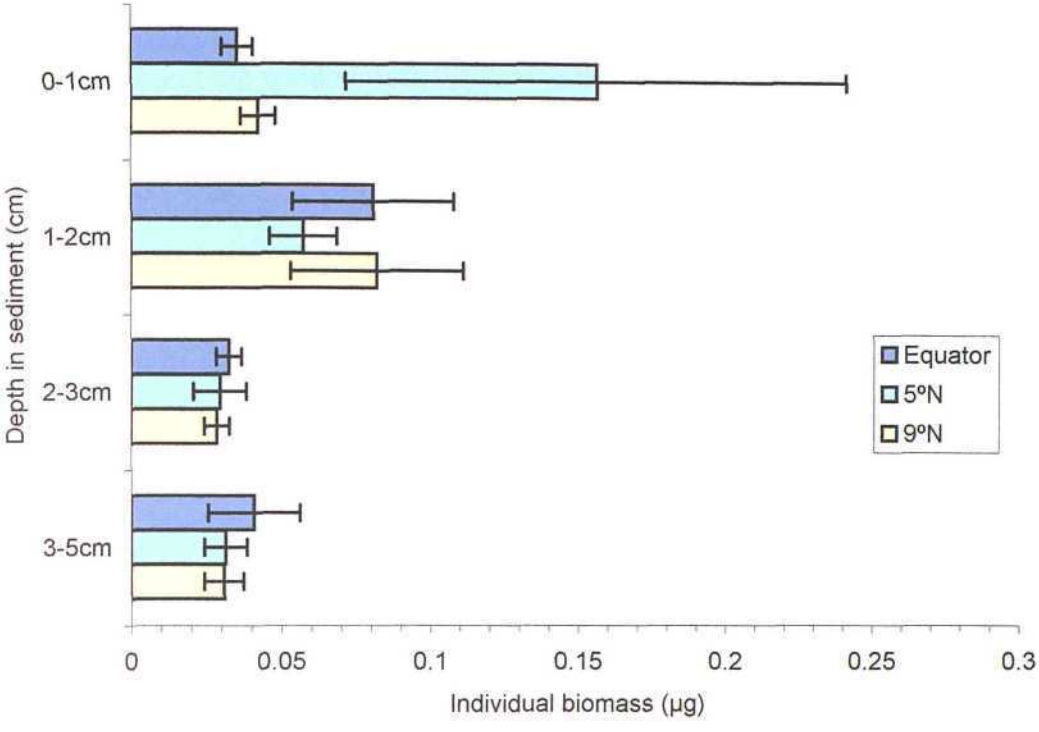


Figure 4.8 Vertical distribution of mean individual biomass with sediment depth for three JGOFS EqPac stations. Error bars are ± 1s.e. Note that 3-5cm sediment layer represents a 2cm layer.



biomass occurred in the surface (0-1cm) sediment layer and then fell by half in the 1-2cm layer. Below the 2cm sediment horizon, individual biomass was not significantly different from either of the other two stations. Between the surface and 5cm depth the decrease in body size followed an exponential curve.

The vertical distribution profiles for abundance and total biomass also permitted examination of the validity of using only the 0-1cm sediment layer for ecological studies such as these. Whole-core abundance and total biomass for the top 5cm were plotted for stations at 0, 5 and 9°N (Figure 4.9). The patterns matched those of the 0-1cm sediment layer so closely that, in this study, it was deemed appropriate to consider the surface sediments to be representative of the sediment core as a whole in terms of abundance and total biomass.

Biomass size spectra were constructed for each sediment horizon at stations 0°, 5° and 9°N along the phytodetrital gradient (Figure 4.10). At the equatorial station the mean size class corresponds to 0.0093 - 0.037 μg. This increased slightly at 5°N in the upper 2 cm to 0.018 - 0.0037 μg, i.e. it increased by one size class. Below the 2cm horizon at 5°N there was a pronounced 'spike' that represents many small individuals. This pattern was repeated throughout the top 5cm of sediment at the 9°N station. Additionally, at 9°N the broad peak that corresponded to larger individuals at stations further south was almost absent, accounting for only 15-17 individuals, compared with roughly one-third of the total number of nematodes measured at the equator. Overall, there was a general trend towards smaller body size that began in the deeper sediment layers at the equator and moved towards the sediment surface with increasing latitude.

Interestingly, the biomass spectra for 5°N appeared to be in contrast to the abundance vs. biomass plot (Figure 4.5). To recall, the abundance vs. biomass plot indicated a shift towards fewer nematodes of greater individual biomass, whereas the biomass spectra do not seem to support this prediction. This may be due to the presence of a few large individuals (which are represented in the biomass spectra) causing skewness in the distribution of biomass amongst individuals.

Figure 4.9 Whole core (0-5cm) (a) abundance and (b) total biomass at three JGOFS EqPac stations. Error bars are ± 1s.e.

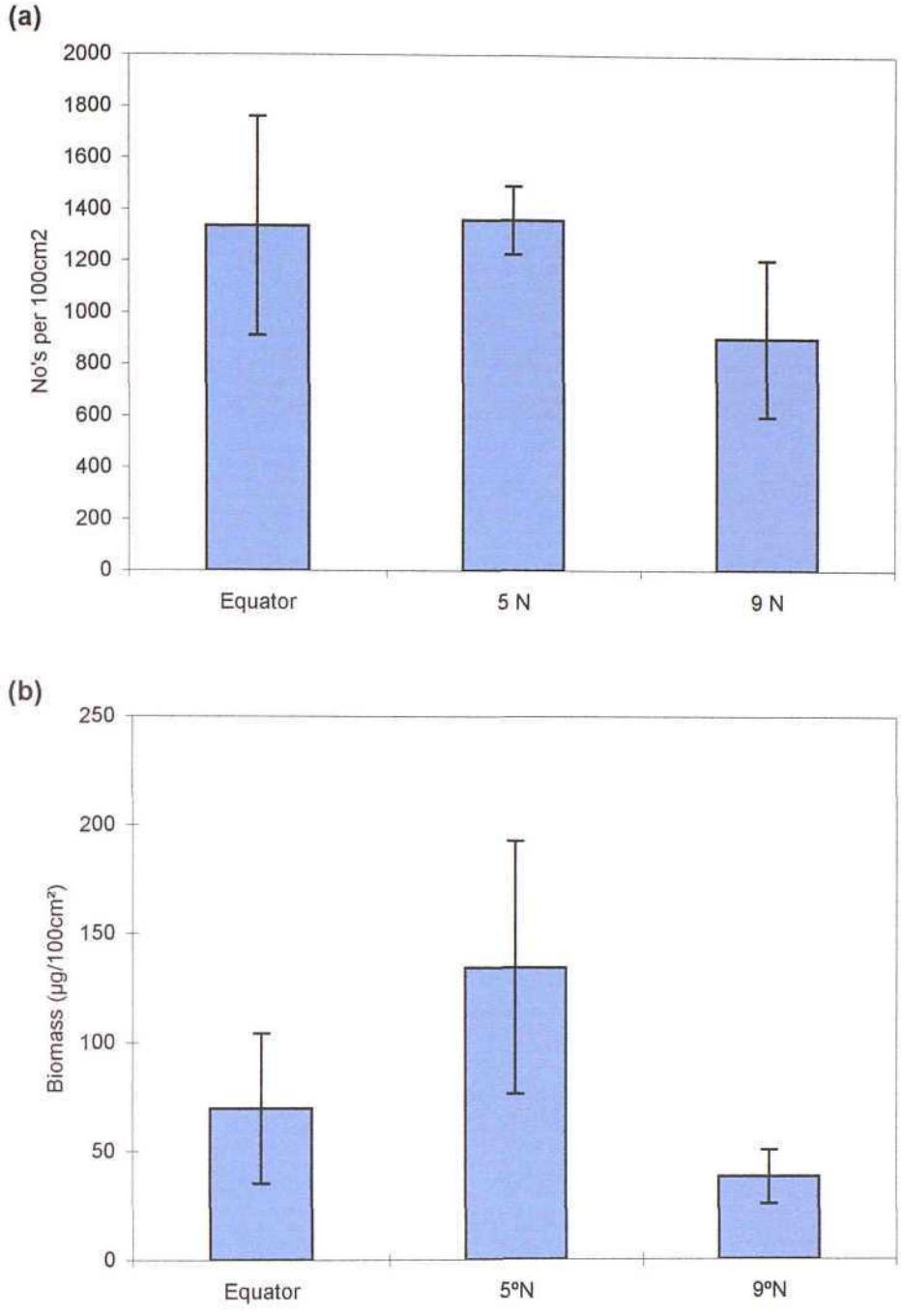
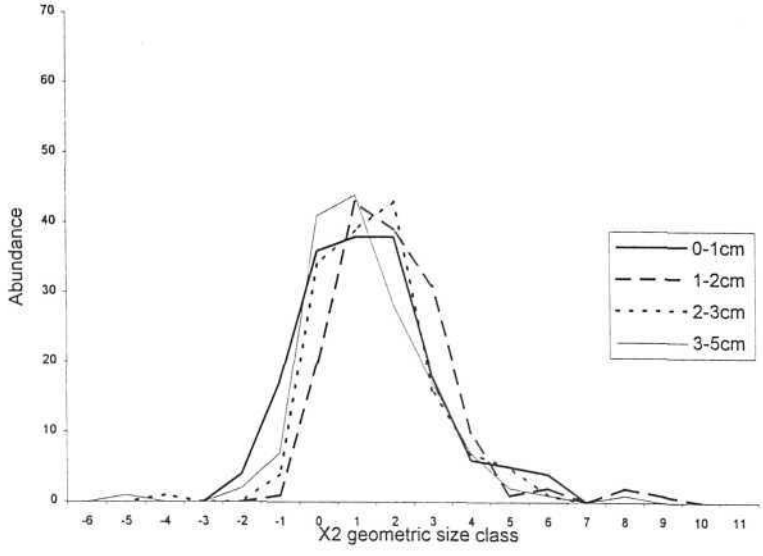
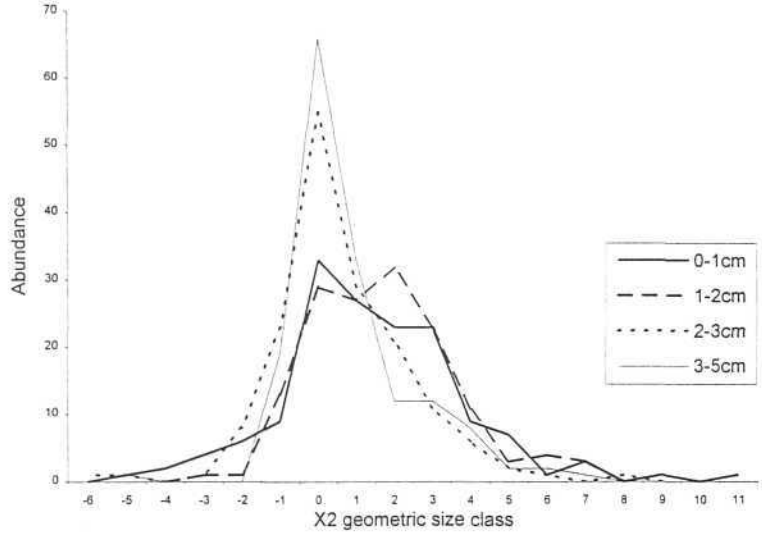


Figure 4.10 (shown overleaf) Abundance-biomass size spectra for three JGOFS EqPac stations. Size spectra for vertical profiles are also shown. X2 geometric size classes are as described by Warwick (1984).

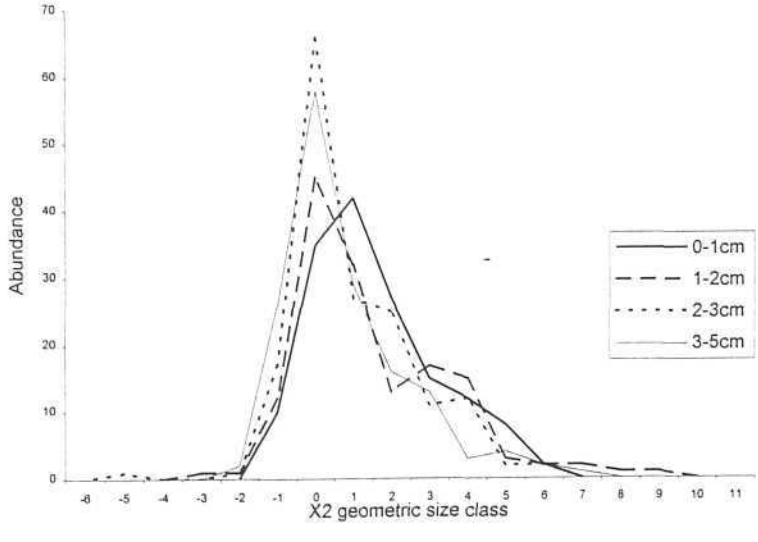
Equator



5°N



9°N



4.3 Discussion

Smith *et al.* (1996) presented a record of the quantity of phytodetritus material overlying the surface sediments of the JGOFS EqPac transect during November to December, 1992 (Smith *et al.*, 1996). This record was based simply on an observational measure of the degree of sediment cover provided by the phytodetritus in multiple-core samples. There was a marked peak at the equator which decreased rapidly with higher latitude to a complete absence at 9°N. At most, only a thin veneer of phytodetrital material was recorded from the seafloor at station ALOHA. A significant increase in nematode abundance and biomass in November-December, 1992, was measured for stations 0-5°N when compared with 9-23°N. However, in contrast to the distribution of phytodetritus, nematode abundance attained its maximum value at 2°N and biomass at 5°N. Furthermore, no significant difference was discernible between the abundance and biomass of nematodes at the equatorial station and those at 9° and 23°N. This would suggest that the presence of phytodetritus at the seafloor was not the primary factor controlling the horizontal distribution of nematode abundance and biomass.

These phytodetritus measurements (Smith *et al.*, 1996) were recorded at the same time that the benthic samples were collected. Chlorophyll *a* has a degradation time-scale of approximately 100 days (Stephens *et al.*, 1997) which suggests that this material has been at the sediment surface for less than 100 days, allowing for sinking time. Sediment trap data (Honjo *et al.*, 1995) suggest that POC flux to the seafloor is highly variable and it seems reasonable to infer that phytodetrital deposition will be similarly variable. Consequently, these phytodetritus measurements potentially do not provide information on the distribution of organic material that may have triggered a response in the nematode populations. To investigate response times, 17-day organic-carbon fluxes into sediment traps approximately 2000m above the seafloor (Honjo *et al.*, 1995) were averaged over increasing time periods prior to the benthic sampling event at 0, 2, 5 and 9°N. Although it is thought that sediment traps do not to collect phytodetrital material accurately (Honjo and Manganini, 1993; Smith *et al.*, 1997), POC flux would similarly be expected to impact nematode populations and may serve as a proxy for phytodetrital input. A high positive correlation ($r = 0.921$, $P < 0.01$) was obtained between total nematode biomass and organic carbon flux averaged over roughly five months (Figure 4.11b) compared with

other time periods (Table 4.4). The correlation between organic carbon flux and nematode abundance (Figure 4.11a) was less pronounced but also occurred best with 153 day flux ($r = 0.784$, $P < 0.01$). No measurement of nematode community generation time has been recorded for deep-sea nematodes, but studies of a number of shallow-water species yield generation times ranging from a few days to several months (for reviews see Heip *et al.*, 1985; Giere, 1993). Therefore, five months would seem to be a reasonable response period. This strong relationship offers further evidence that supply of organic material does limit the horizontal or temporal distribution of nematode populations in the deep sea as proposed by Shirayama (1984a).

In addition, there was also a high positive correlation between nematode abundance and microbial biomass ($r = 0.931$, $P < 0.01$, Figure 4.12a), although nematode biomass was not as strongly correlated ($r = 0.695$, n.s., Figure 4.12b) and the reasons for this are unclear. A high proportion of the nematodes along the JGOFS EqPac transect are selective deposit feeders (see Chapter 5) and hence such a strong correlation is to be expected. These nematodes are predominately small-sized individuals and so do not contribute greatly to community biomass. It is hypothesised that the elevated microbial biomass, acting as a food source for these animals, triggers a reproductive response in the nematode communities at 0-5°N, thus explaining the elevated nematode densities at these stations. It is also proposed that larger nematodes, which contribute a greater proportion of the total biomass may actually consume the phytodetritus directly (Jensen, 1987). If POC flux does serve as a proxy for phytodetrital input this may explain the observed correlation between nematode biomass and 5-month POC flux.

Abyssal meiofauna have been studied from only a small number of other locations in the Pacific and nematode density and biomass have been recorded from only two of these (Table 4.5). Neither of these locations are reported as receiving a phytodetrital input. However, the Clarion-Clipperton fracture zone is located at 14°N, 130°W and, as expected, the density of nematodes at the 9° and 23°N stations falls within the range recorded by Renaud-Mornant and Gourbault (1990). Unfortunately, no values for nematode biomass were cited in their report, but values across the JGOFS EqPac transect fall within the range recorded off Japan in the western Pacific (Shirayama, 1984a).

Figure 4.11 (a) Abundance and (b) total nematode biomass for 0-1cm sediment layer correlated with organic carbon flux averaged over 5 months prior to benthic sampling event. Organic carbon flux values are taken from Honjo *et al.* (1995) except 23°N which was taken from Smith *et al.* (1997). Only an annual POC flux value was available for this station. Error bars are ± 1s.e. Regression line equations are shown on the chart.

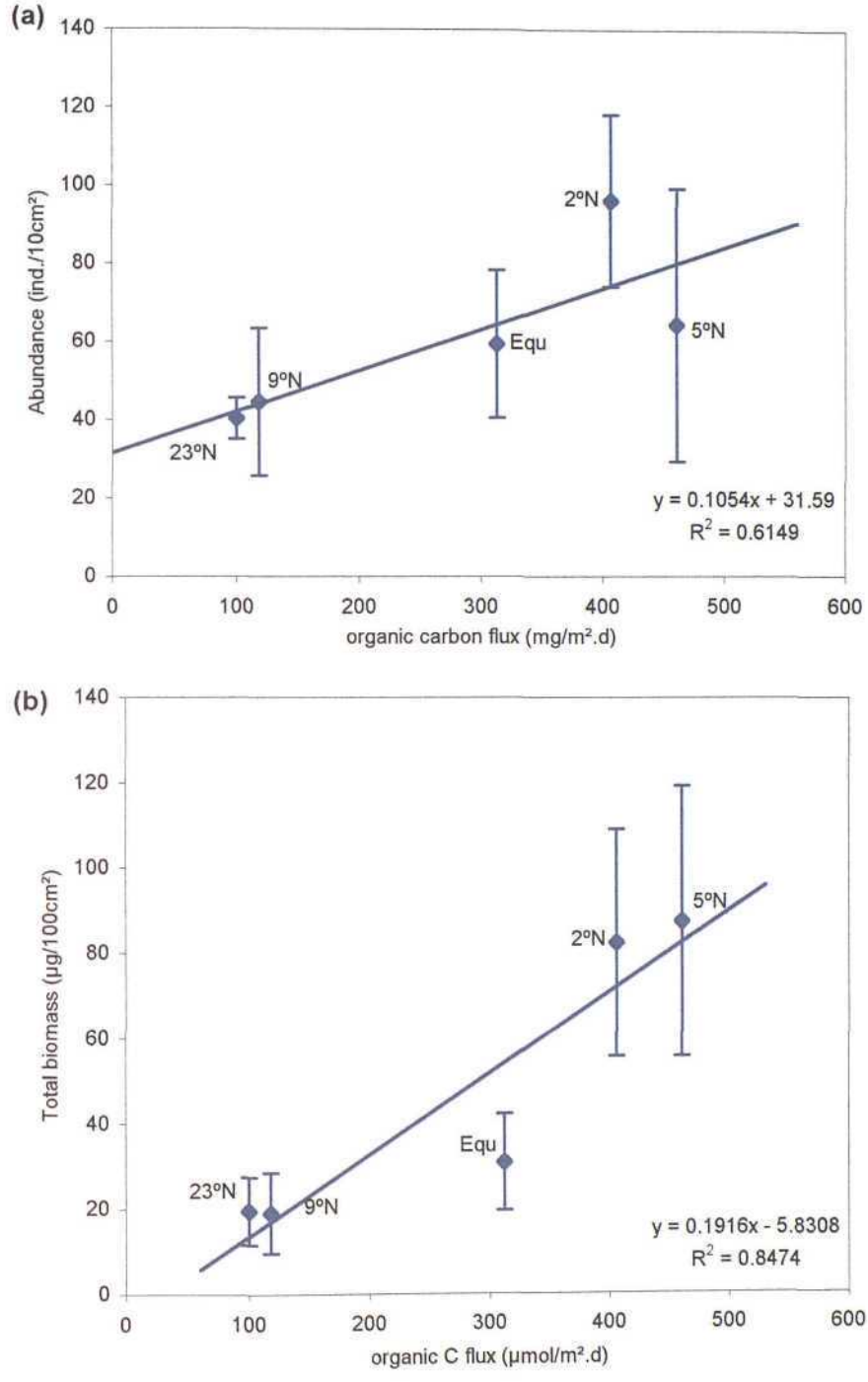


Figure 4.12 (a) Abundance and (b) total nematode biomass for 0-1cm sediment layer correlated with microbial biomass. Microbial biomass values are taken from Smith *et al.* (1998). Error bars are ± 1s.e. Regression line equations are shown on the chart.

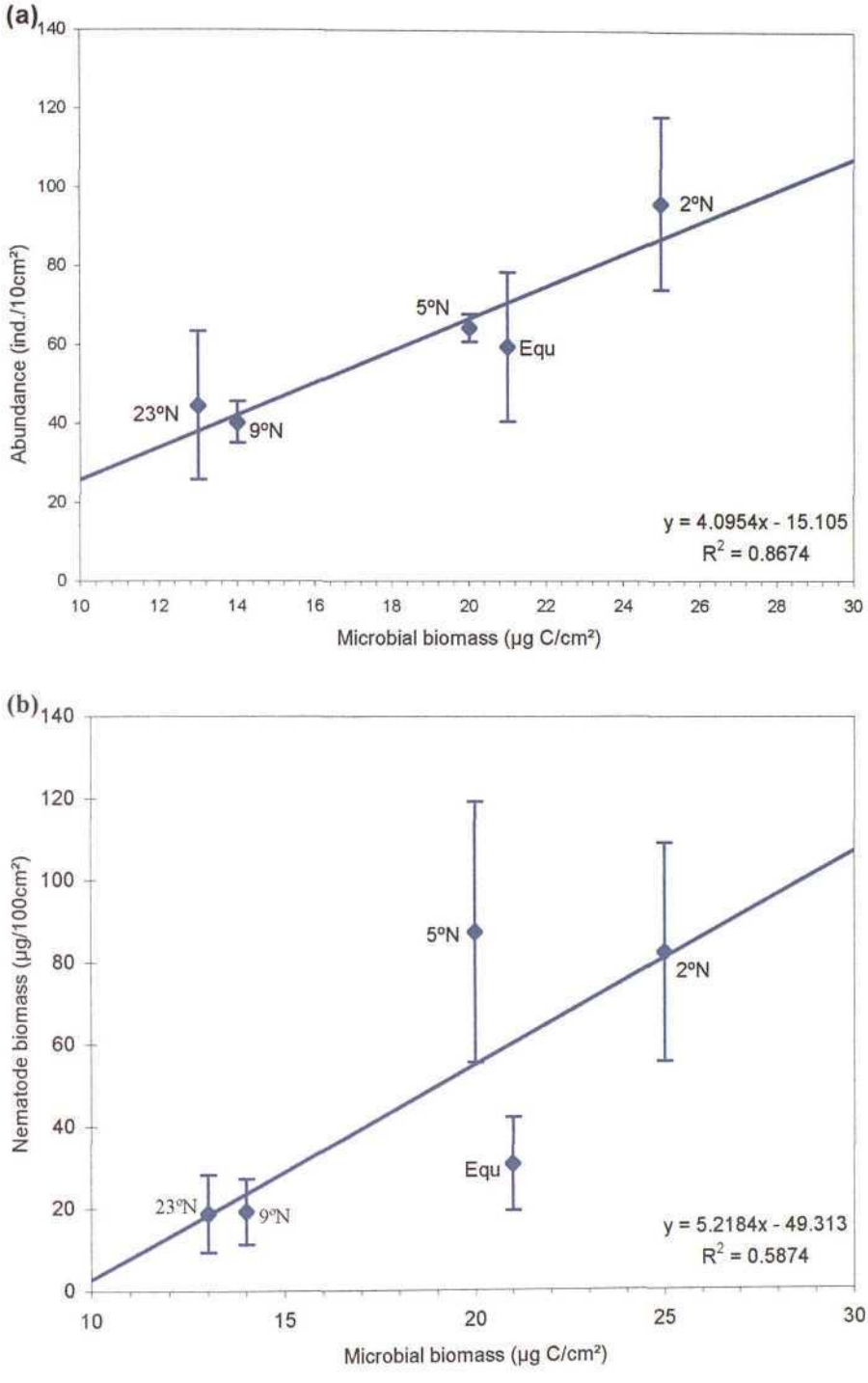


Table 4.4 Comparison of Pearson correlation values (r) for regression of mean nematode biomass vs POC flux (mg/m².d) integrated over increasing time periods for staions at 0, 2, 5 and 9°N

Latitude	Nematode biomass (µg/100cm²)	34d	51d	68d	85d	102d	136d	153d	170d	187d	1 year
Equator	30.753	507.5	472.67	360.25	305.4	282.83	266.38	312.67	354.4	391.33	374.3
2°N	82.346	307	254	244.75	207.2	253.5	333	406.33	368.7	374.27	330.29
5°N	87.36	487	426	451.5	487.8	540	489.25	460.67	444.2	436.91	332.05
9°N	18.895	76	74.33	94.5	9838	101.33	113.13	118.22	124.2	134.45	125.95
r	-	0.443	0.356	0.576	0.679	0.736	0.89	0.91	0.797	0.718	0.54

The EqPac values seem surprisingly low when compared with abundance and biomass values recorded from sites in the NE Atlantic that receive a seasonal pulse of phytodetritus, although they do fall within the ranges recorded (Table 4.5). These low values may be due to the much greater quantity of phytodetrital material that arrives at the seafloor in the NE Atlantic. In the Porcupine Seabight for example, phytodetritus can occur in uniform greenish carpets up to 1cm thick (Billett *et al.*, 1983; Lampitt, 1985; Hecker, 1990) and the phytodetritus standing crop can attain 32 mmol organic C .m^{-2} at the BIOTRANS site (at 47°N, 20°W, close to the Porcupine Seabight, 50° N, 13° W) during the spring bloom event (Thiel *et al.*, 1988/89). In the equatorial Pacific, the maximum standing crop of phytodetritus reached only 2.6 mmol organic C.m^{-2} (Smith *et al.*, 1996) and the phytodetritus appeared as patchy, gelatinous aggregates that become trapped in surface pits and furrows, or as a very thin veneer. In addition, POC flux during the spring bloom in the NE Atlantic attained a maximum of 240 mg.m^{-2} day^{-1} (at 48°N 21°W, Honjo and Manganini, 1993) compared with a maximum of 162.6 mg.m^{-2} day^{-1} (Honjo *et al.*, 1995) in the equatorial Pacific.

This very patchy distribution of phytodetritus may also offer an explanation for the high intra-station variability expressed in the 0-5°N samples. Patchy aggregations of deep-sea meiofauna are well documented (see review in Rice and Lambshead, 1994) and phytodetritus has been postulated to be a causative agent. Lambshead and Gooday (1990) demonstrated that heterogeneity in foraminiferal assemblages increased following a phytodetrital pulse in the NE Atlantic. There is also evidence for the migration of nematodes, particularly the smaller Monhysteridae which are primarily bactiverous, into the flocculent phytodetrital material (Thiel *et al.*, 1988/89). Similarly, elevated meiofaunal abundances were measured in the immediate vicinity of abandoned polychaete burrows (Aller and Aller, 1986) that had trapped organic material. This was termed *resource-driven aggregation* by Lambshead and Hodda, (1994), and Rice and Lambshead (1994). They suggested that as resource availability increases so does abundance and the animals correspondingly become more aggregated around these resources. Dense aggregations of nematodes may therefore be expected in the sediments of the 0-5°N stations as a consequence of well-developed phytodetrital accumulations.

Table 4.5 Comparison of nematode abundance and biomass perviously recorded from sites in the Pacific and eastern Atlantic Oceans (* = seafloor recieves a significant input of phytodetritus, - = not recorded)

Location	Water depth (m)	Abundance (ind./10cm²)	Biomass (µg/100cm²)	Reference
W Pacific	5580-5820	29-95	60-365	Shirayama, 1984
Clarion-Clipperton fracture zone, eastern, central Pacific	4905-5140	10-78	-	Renaud-Mornant and Gourbault, 1990
Station ALOHA, central Pacific	4871-4884	28-49	8-43	This study
JGOFS EqPac transect *, eastern central Pacific	4301-4991	20-160	4-184	This study
Poprcupine Seabight *, NE Atlantic	4167-4850	272-462	-	Pfannkuche, 1985
Porcupine Abyssal Plain *, NE Atlantic	4843-4850	95-158	135.4	Lambshead *et al*, 1995
BIOTRANS *, NE Atlantic	4330-4561	56-229	-	Soltwedel *et al*, 1996
DORA *, NE Atlantic	4000-4800	101-985	111-164	Rutgers van der Loeff and Lavaleye, 1986
Angola Basin *, eastern central Atlantic	4474-4601	323-425	-	Soltwedel and Thiel, 1995

The significant grouping of stations 0-5°N in terms of nematode abundance and biomass corresponds well to the patterns of POC flux into sediment traps (Honjo *et al.*, 1995) and the occurrence of concentrations of buoyant diatom species such as *Rhizosolenia* (Yoder *et al.*, 1994) in the surface waters between 2° and 5°N (Flament *et al.*, 1996). Smith *et al.* (1996) proposed that these concentrated diatom patches form dense phytodetrital aggregates that settle rapidly to the seafloor. Tropical instability waves (TIWs) generated at the convergence zone intensify the patches and oscillate about 2°N. TIWs are common throughout early summer to (Yoder *et al.*, 1994) and substantial increases in POC and opal flux were reported (Honjo *et al.*, 1995) during an intense TIW period (August – October, 1992) that occurred prior to the benthic sampling programme (November – December, 1992). Strong meridonal waves (up to 60 $cm.s^{-1}$) associated with passing TIWs distribute settling aggregates over a broader latitudinal band that extends south to 2°S (Murray *et al.*, 1994; Yoder *et al.*, 1994; Honjo *et al.*, 1995). The start of the TIW period also corresponds well to the 5-month response time demonstrated in the nematode communities at 0-5°N.

Vertically in the sediment, few changes in the distribution of abundance or biomass are apparent with increasing latitude in the EqPac data. Abundance and biomass values are generally lower at 9°N, which may simply be attributable to the reduced organic-carbon input to the sediment surface. In addition, a substantially greater proportion (78%) of the total 0-5 cm biomass is found in the 0-1 cm layer at 5°N, compared with the equator and 9°N stations (41 and 50% respectively). Following a food input at a sublittoral site, an upward migration of meiofauna was observed (Shulz, 1983, in Graf, 1992). Previous studies in the NE Atlantic have not confirmed this 'shoaling' effect (Lambshead *et al.*, 1995; Gooday *et al.*, 1996). However, in the current study, the absence of significantly increased numbers, but increased biomass in the 0-1cm layer at 5°N, suggests movement by a few large individuals to take advantage of the increased food availability in the surface sediments.

Unfortunately, limited data regarding the vertical distribution of bacterial biomass or labile organic compounds from the study locations have been published. Stephens *et al.* (1997) noted that chlorophyll *a* had largely disappeared by 1.5 cm sediment depth. Concentrations of chloroplastic pigments were greatest at the 2°N station but as already discussed, this represents a depositional event that may have occurred too recently to have

triggered a metazoan response. Similarly, excess ^{234}Thorium (^{234}Th) activity decreased with sediment depth; at depths between 2 and 3cm excess ^{234}Th activity was generally not detected unless measurements impinged on burrow complexes partially filled with phytodetritus (Pope *et al.*, 1996). ^{234}Th is scavenged by phytodetritus as the particles sink through the water column (Fowler and Knauer, 1986) and consequently recently-settled phytodetrital material has high excess activities (Smith *et al.*, 1996). As ^{234}Th has a signal decay of ~100days after particles reach the seafloor (Aller and DeMaster, 1984), it is useful for indicating recent arrival and burial of phytodetrital material. As such, it is likely to provide good indication of food availability within the sediments (Stephens *et al.*, 1997).

Profiles of both chloroplastic pigments and excess ^{234}Th activity appear to closely match the vertical distribution of nematode abundance and biomass; all exhibit maxima in the surface layer and a marked decline below the 2cm horizon. Previous studies have demonstrated a close correlation between nematode standing stock and chloroplastic pigment proxies for food availability (Pfannkuche, 1985; Pfannkuche and Thiel, 1987; Soetaert and Heip, 1989; DeBovée *et al.*, 1990; Soltwedel and Thiel, 1995; Soetaert *et al.*, 1997). The current study offers further evidence in support of the hypothesis that food availability governs nematode vertical distribution.

Contrary to ^{234}Th excess activity profiles, there is no evidence (in the present study) for the presence of a subsurface peak in nematode abundance or total biomass. However, there is a marked sub-surface peak in mean individual biomass at the equator and 9°N. It has been demonstrated that, in high food concentration zones, large animal bioturbation activity would be high, mixing incoming food deeper into the sediment (Pope *et al.*, 1996; Smith *et al.*, 1997). Thiel (1983) argued that meiofaunal distribution should reflect this, exhibiting sub-surface peaks in areas of high bioturbation. Studies on the Porcupine Abyssal Plain appear to reinforce this hypothesis (Lambshead *et al.*, 1995). Similarly, the nematodes of the equatorial samples are largest deeper in the sediments. This is also in good agreement with the surface distribution of biomass; total biomass and mean individual biomass were greatest at 5°N, which received the highest input of POC flux over the 5-month response period. This was attributed to the increased occurrence of

larger nematodes which are thought to feed directly on phytodetritus. However, the vertical distribution of density and total biomass are in disagreement with this theory.

In a comprehensive study of the biotic and abiotic factors influencing the vertical distribution of nematode abundance and biomass, Shirayama (1984b) indicated that oxygen availability was the primary factor limiting the maximum depth of meiofaunal distribution in abyssal sediments off Japan. In the sediments of the equatorial Pacific, pore-water oxygen concentrations were about 170 μM at the surface, declining exponentially to about 50μM at 5cm depth at the equator, and to about 150μM at 5cm at 9°N (Hammond *et al.*, 1996). Pore water oxygen profiles exhibited much smaller gradients with increasing distance from the equator, and Hammond *et al.* (1996) attributed this to the increased POC flux and phytodetrital input at the 0-5°N stations. Nematode abundance and biomass profiles in the same sediments, however, did not demonstrate such dramatic differences in gradient and it is concluded that at the sediment depths examined (0-5cm) pore-water oxygen concentration does not appear to be influencing the distribution of nematodes. Oxygen concentrations of 6μM in the water overlying the sediments were not thought to be affecting the abundance of nematodes in a study in the San Diego Trough (Lambshead *et al.*, 1994). It is suggested, however, that deeper in the sediment, oxygen concentrations would be expected to play a greater role in structuring the vertical abundance and biomass profiles.

It is argued that the high intra-station variability in abundance and biomass at the equator and 5°N might reflect a greater degree of mega- and macrofaunal sediment reworking. Megafaunal and macrofaunal standing stocks are both highest at the equator (Smith *et al.*, 1997). Urchins are the most abundant mobile megafauna from 0 to 5°N and they burrow partially submerged in the sediment to depths of 2-3cm. They were not recorded at 9°N (Hoover *et al.*, 1994). A secondary effect of urchin burrowing is that the furrows act to trap and concentrate phytodetrital aggregates (Smith *et al.*, 1996) which would cause localised enhancement of nematode standing stocks in the surface sediments. Hoover (1995) estimated that urchins reworked 15-20% of the seafloor between 0 and 5°N per year and consequently would be expected to have some effect on meiofaunal populations on a localised scale. However, in conjunction with the proposed 5-month response time of nematode communities, this sediment turnover time may occur on a time-scale too great to

significantly impact nematode populations except at the decimetre scale. This may explain the high degree of between-core, intra-station variability observed in the 0-1cm layer at the 2-5°N stations.

In addition to an increase in total nematode biomass, there is a shift in biomass size spectra towards an increase in mean individual body size with increasing POC flux to the seafloor. Over twenty years ago, Thiel (1975) proposed that "Associations governed by constantly limiting food availability are composed of small individuals on average". This concept was originally based upon the widespread observation that the meiofauna increased in importance relative to the macrofauna with increasing water depth, but may also explain the overall mean body size of deep-sea nematodes (Jensen, 1988). Some studies have been based upon comparisons of the fractions of fauna retained upon sieves of decreasing mesh sizes. For example, Pfannkuche (1985) found a significant increase in the abundance of nematodes in the 46-60μm fraction and a corresponding decrease in the >150μm size fraction with increasing depth in the Porcupine Seabight. This was attributed to the decrease in food availability with increasing depth. Similarly, along a depth gradient in the Mediterranean, not only the arithmetic mean size of nematodes, but also the median, geometric mean and modes of length and weight spectra decreased with decreasing organic supply (Soetaert and Heip, 1995). The results of two studies of nematode size spectra from a number of locations in the NE Atlantic, including two locations receiving significant inputs of phytodetritus, also confirmed the dominant controlling effect of food supply on nematode size (Vanreusal *et al.*, 1995; Soltwedel *et al.*, 1996). The results from this study are also in agreement with Thiel's (1975) hypothesis. There is a clear general trend for increasing densities of smaller-sized individuals with decreasing food availability and also a corresponding decrease in the numbers of larger-sized nematodes.

The increasing abundance of smaller-sized individuals deeper in the sediment is in contrast to previous studies. Soetaert and Heip (1989) noted an increase in mean body length at a deep-water (1200m) site in the Mediterranean Sea and Jensen (1983) described three sediment layers in the Öresund (28m): the upper centimetre was dominated by small nematodes (0.42 μg dry weight), the intermediate layer (2-4cm) was dominated by large nematodes (0.73 - 1.05μg dry weight) and below 4 cm the smaller nematodes returned. Vivier (1978) also noted a more frequent occurrence of larger worms deeper in the

sediment. It is possible that the nematodes of the JGOFS EqPac stations are dominated by a juvenile-rich, adult-rare age structure and this would explain the high proportion of smaller nematodes. This type of community age-structure was proposed to occur in food-rich areas where reproductive turnover would be high, in contrast to food-limiting areas where the energetic costs of reproduction cannot be met (Soltwedel *et al.*, 1996). The results are also in agreement with Thiel's (1975) hypothesis that would predict greater numbers of smaller individuals deeper in the sediment where food availability is reduced. Chlorophyll *a* profiles and ^{234}Th profiles indicate that these tracers are absent from the sediment by 2cm depth (Pope *et al.*, 1996; Smith *et al.*, 1996) and sediment labile organic content is also dramatically reduced at this depth (Hammond *et al.*, 1996).

Without further studies at a lower taxonomic level to determine reproductive strategies of the nematode communities at these locations, it is impossible to state whether it is the amount of organic material that is directly controlling organism size or whether the results are expressing the reproductive phase of the nematode lifecycles. It is possible that the correlation between body size and POC flux represents a predominately *K*-species life history in the EqPac nematode communities. *r*-strategists typically respond to elevated food input with a high reproductive output whereas the food input is more likely to be used for somatic growth in *K*-strategists (MacArthur and Wilson, 1967; Pianka, 1970). Populations are generally structured by competitive interactions and the organisms are generally slow-growing with larger body sizes, compared to *r*-strategists. Little is known of the life-history of deep-sea nematodes but the high diversity that has been recorded in other studies (Tietjen, 1984; Thistle and Sherman, 1985; Tietjen, 1989; Boucher and Lambshead, 1995) would predict such a strategy.

4.4 Conclusions

- Examination of the distribution of nematode abundance and biomass indicates that elevated POC flux into sediment traps is correlated with a significant increase in abundance, total biomass and mean individual biomass between 0 and 5°N in the equatorial Pacific.

- Previous work failed to show a metazoan response to elevated POC flux as a result of using time-scales appropriate for shallow-water nematodes. The current study suggests that abyssal nematodes respond on a five-month time-scale in the equatorial Pacific, roughly 4-5 times longer than measured in shallow water nematodes (Heip *et al.*, 1985).

- The vertical distribution of EqPac nematodes followed a similar profile at all sites regardless of location. It is suggested that this may indicate an absence of bioturbation effects by larger organisms, in contradiction to earlier work in the NE Atlantic (Pfannkuche, 1992; Gooday *et al.*, 1996).

- The increase in POC flux into sediment traps was correlated with an increase in mean body size rather than an increase in numbers, suggesting that the *K*-strategy life-history may prevail in abyssal nematode communities in the equatorial Pacific.

5.1 Introduction

One of the primary reasons that nematodes perhaps do not receive the ecological attention that such a well-represented member of the benthos deserves, is their enormously difficult taxonomy. Incomplete taxonomic literature and poor descriptions of many genera and species compound problems with small size and huge arrays of species. These problems, to some extent, can be overcome by the use of analytical methods that make direct use of some general ecological principle. One such method of analysing complex nematode assemblages uses functional groups. These groups are based upon morphological distinctions that are thought to imply similarity in an important ecological function (Jumars and Fauchald, 1977).

Wieser (1953) originally proposed that the structure of the buccal cavity could be used to separate nematodes into four groups that imply different feeding mechanisms: 1A = small/absent buccal cavity with no buccal armature; 1B = moderately-sized buccal cavity with no buccal armature; 2A = moderately-sized buccal cavity with small teeth and 2B = large buccal cavity with large teeth and/or mandibles (see chapter 3). This classification has subsequently been utilised in many shallow-water studies (see reviews in Heip *et al.*, 1985; Jensen, 1987) and, more recently, in the deep sea (Thistle and Sherman, 1985; Jensen, 1986; Rutgers van der Loeff and Lavaleye, 1986; Jensen, 1988; Tietjen *et al.*, 1989; Soetaert and Heip, 1995; Thistle *et al.*, 1995).

Wieser (1953) suggested four functions for his feeding groups: 1A = selective deposit feeders; 1B = non-selective deposit feeders; 2A = epistrate feeders and 2B = predators (Wieser, 1953) or omnivores (Wieser, 1960). Groups 1A, 1B and 2A all feed on bacteria , unicellular algae and fungi according to Jensen (1987), but the deposit feeders, lacking buccal armature, feed only by means of the sucking power of the oesophagus. Selectivity is implied by the differing sizes of the buccal cavity restricting the range of particle sizes that can be handled. The 2A-epistrate feeders use their small teeth to either scrape food materials off larger particles or pierce or crack a food object, such as a diatom cell, and ingest the cell liquid by oesophageal pumping activity (Tietjen and Lee, 1977). Wieser's

schema appeared to be supported by occasional observations of gut contents (e.g. Perkins, 1958; Hopper and Meyers, 1967; Deutsch, 1978), although gut analyses of small organisms are generally inadequate (McIntyre, 1969; Tietjen, 1969) as only the hard, more indigestible items are recognisable.

Subsequent observations on the feeding behaviours of shallow-water (Tietjen and Lee, 1977; Lopez *et al.*, 1979; Jensen, 1982; Romeyn and Bouwman, 1983; Bouwman *et al.*, 1984; Jensen, 1986; Jensen, 1987; Moens and Vincx, 1997) and deep-sea nematodes (Jensen, 1992) have not entirely supported the originally-suggested feeding modes of Wieser's groups. For example, some species with a 1A-type buccal cavity were reported to feed non-selectively (Romeyn and Bouwman, 1983) and some with a 1B-type buccal cavity utilise sensory appendages to select suitable food particles out of a majority of similar-sized inedible particles (Bouwman *et al.*, 1984). Studies of some 2B-type oncholaimids indicate that adults are only partially predatory and juveniles utilise dissolved organic material (DOM) (Lopez *et al.*, 1979) whilst 2B-type sphaerolaimids capture live prey (Jensen, 1992).

As a consequence of these studies some significant alterations were proposed. Romeyn and Bouwman (1983) discriminated between two major feeding strategies; selective and non-selective, and argued that cephalic setation and oesophageal pumping activity should be included in the creation of feeding groups. Jensen (1986) rejected the division of group 1 into selective and non-selective deposit feeders based upon the absence of experimental evidence demonstrating that a nematode with a small buccal cavity is more selective in its ingestion of food than a nematode with a larger buccal cavity. Jensen (1987) subsequently argued that the 2B group be divided into true predators which catch living prey by protusible jaws or mandibles (as in the Thoracostomopsidae, Enopliidae and Selchinematidae), and scavengers which feed on dead animals or suck the contents from injured animals whilst releasing enzymes (e.g. Oncholaimidae and Encheliidae).

In this study, Wieser's (1953) original buccal-morphology groups have been used, based upon the morphological divisions he described. However, the allocation of particular genera into feeding groups as listed in Wieser's (1953) paper have not been utilised. Previous deep-sea workers have adopted the same strategy (Thistle and Sherman, 1983;

Thistle *et al.*, 1995). The subdivision of group 1 was retained for the following reasons: (1) their relative proportions in some organically-enriched as opposed to un-enriched sediments (Vincx, 1989; Smol *et al.*, 1991) suggests some ecological significance; (2) significant seasonal differences in the abundance of selective and non-selective nematodes (Moens and Vincx, 1997) suggest resource partitioning and (3) analysis of functional groups in the deep sea (Thistle *et al.*, 1995) offers further support for this subdivision. In addition, although Jensen (1986; 1987) provides a strong argument for the subdivision of group 2B into predators and scavengers, at the EqPac sites individuals from these groups were rare. Consequently, the 2B group was retained intact for statistical purposes. This grouping has been employed in previous deep-sea studies by Thistle *et al.* (1995).

Thistle and Sherman (1985) proposed that tail shape could also provide a basis for erecting nematode functional groups. The tail plays an important biological role in locomotion (Adams and Typer, 1980), feeding (Riemann and Schrage, 1978) and possibly reproduction (Lambshead, *pers. comm.*). It has been argued that the male wraps the tail around the female, using caudal supplements to ensure correct positioning of the copulatory apparatus. The major variations in nematode tails are their shape, and the presence or absence of caudal glands. All of the EqPac nematodes possess caudal glands so their division was restricted to tail shape. Thistle and Sherman (1985) created 11 arbitrary, morphological tail-shape groups based upon specimens from a deep-sea site on the Scotian Rise, but Thistle *et al.* (1995) subsequently decided that, due to the overlap of some categories, this number could be reduced to four. The four tail shape groups recognised were (1) rounded tail with a blunt end, (2) clavate-conicocylindrical; initially conical with extension to the tip, (3) conical, with pointed tip and tail length less than five body-widths and (4) long with tail length greater than five body widths (Thistle *et al.*, 1995 – see chapter 3, section 3.1.7). The same tail shape categories have been employed in the current study to detect differences between the EqPac sites that may not be reflected in the buccal-morphology groups.

Thistle *et al.* (1995) also proposed combining the tail shape grouping and buccal-morphology grouping to give a two-way classification analogous to that for polychaetes (Jumars and Fauchald, 1977). This two-way analysis (Thistle *et al.*, 1995) revealed an absence of certain combinations from their study sites, for example 2B with short tails,

that are known from other locations (e.g. *Comesa, Pontonema* in shallow waters). The present study set out to test the two-way classification on EqPac nematodes to determine whether additional, ecologically-useful information may be generated.

Phytodetritus is assumed to play an important role in the nutrition of many deep-sea organisms, including nematodes. Analysis of the phytodetrital material from 0-2°N demonstrated the presence of relatively intact pennate and centric diatoms, in addition to large numbers of miscellaneous microalgae. Measurements of glutamate uptake indicated that the EqPac phytodetrital material supported an especially active microbial population (Smith *et al.*, 1996). In contrast, the surface fluff found at 9°N appeared to be substantially more degraded (and similarly for the surface veneer recorded at 23°N, Smith *pers. comm.*) with few, if any, intact diatom remains. In addition to changes in phytodetritus quantity and quality with latitude, the sediments of the EqPac stations also vary, mirroring the productivity of the overlying surface waters. The sediments at stations 0-5°N contained about 80% $CaCO_3$ (Berelson *et al.*, 1994) primarily in the form of foraminiferal tests, whereas at 9°N the sediment was composed mostly of clay with a "soupy" consistency. Some manganese nodules were present (Stephens *et al.*, 1997).

This suggests that the phytodetrital gradient along the 140°W transect offers a variety of food types and microenvironments to nematodes, which would be expected to impact the trophic structure of their communities. Nematodes from the four EqPac stations and also from station ALOHA were assigned to both feeding and tail-shape groups. The functional group composition of nematode communities of the equatorial Pacific was used to test the following hypotheses:

- Elevated POC flux and its associated environmental variables (i.e. bacterial content, sediment type) are not correlated with the trophic composition of EqPac nematode communities

- Bioturbation effects by larger organisms are not correlated with the vertical structure of nematode functional groups

5.2 Results

The feeding groups and tail-shape designations for all stations at all sampling intervals are detailed in Appendices A and B.

5.2.1 Horizontal and vertical distribution of feeding groups

The distribution of individuals between feeding groups was markedly uneven in the 0-1cm sediment layer along the JGOFS EqPac transect, with most individuals belonging to groups 1A, the selective deposit feeders and 2A, the epistrate feeders (Table 5.1, Figure 5.1). This heterogeneity was confirmed in the row-by-column analysis of frequency (G-test statistic = 55.715, d.f. = 12, $\chi^2_{0.001[12]} = 32.91, P < 0.001$). There appeared to be no clear general trend for either increasing or decreasing numbers in any group with increasing latitude, although 2A's, the epistrate feeders, occurred in greatest numbers at 5°N and the occurrence of 2B-type nematodes was highest at the equator. However, the results of multiple Kruskal-Wallis tests for each feeding group indicated that a significant change with increasing latitude occurs only in group 1B ($P = 0.010$).

The 1A selective deposit feeders and 2A epistrate feeders were also the most speciose groups at all sites along the EqPac transect in the 0-1cm sediment layer. Within the 1A group proportionally more species occurred at the 0-5°N stations than at the 9-23°N stations (Table 5.2). However, the proportion of species in the 2A group increased with increasing latitude. The 2B group decreased in species richness with increasing latitude.

Vertically in the sediment, stations at 0 and 5°N exhibited sub-surface maxima in the abundance of 1As, whereas the maximum abundance of this feeding group occurred at the surface at 9°N (Figure 5.2). Type 2A increased in importance with sediment depth at all stations along the transect. Conversely, 2Bs decreased with depth in the sediment at stations 0 and 5°N, although there was a suggestion of a sub-surface maximum at the 1-2cm horizon at 9°N. The abundance of type 1B feeding types seemed to vary with both sediment depth and latitude.

Table 5.1 Mean surface (0-1cm) trophic composition (± 1s.e.) using the trophic groups of Wieser (1953) and Kruskal-Wallis test statistic, Z (tested for proportional abundance of each trophic group).

	Equator	Z	2°N	Z	5°N	Z	9°N	Z	23°N	Z	*P*
1A	64.4 ± 4.523	0.54	56.5 ± 4.555	1.21	60.8 ± 4.630	-1.57	67.67 ± 5.925	0.65	66.75 ± 3.092	-0.67	0.404
1B	2.8 ± 0.8	-1.03	3.75 ± 0.629	0.45	1.4 ± 0.748	-2.48	4.3 ± 1.667	0.35	9.25 ± 1.601	3.05	0.01
2A	24 ± 3.391	-0.41	18.75 ± 3.473	-1.34	35.2 ± 4.212	2.31	24.67 ± 4.256	-0.3	24 ± 1.732	-0.45	0.206
2B	2.4 ± 0.678	1.28	1.5 ± 0.5	0.63	1.4 ± 0.510	-0.21	0.67 ± 0.333	-1.06	1.75 ± 0.75	-0.85	0.531

Figure 5.1 Nematode feeding-group composition for the surface (0-1cm) sediment layer along the EqPac transect. Based on the diagrammatic feeding groups of Wieser (1953) who suggested that 1A = selective deposit feeders, 1B = non-selective deposit feeders, 2A = epistrate feeders and 2B = predators/omnivores.

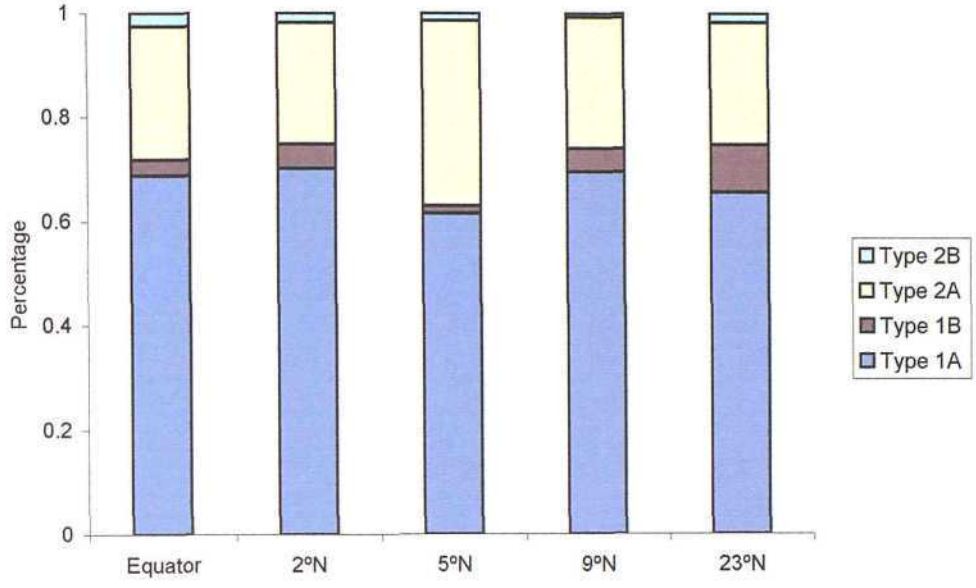
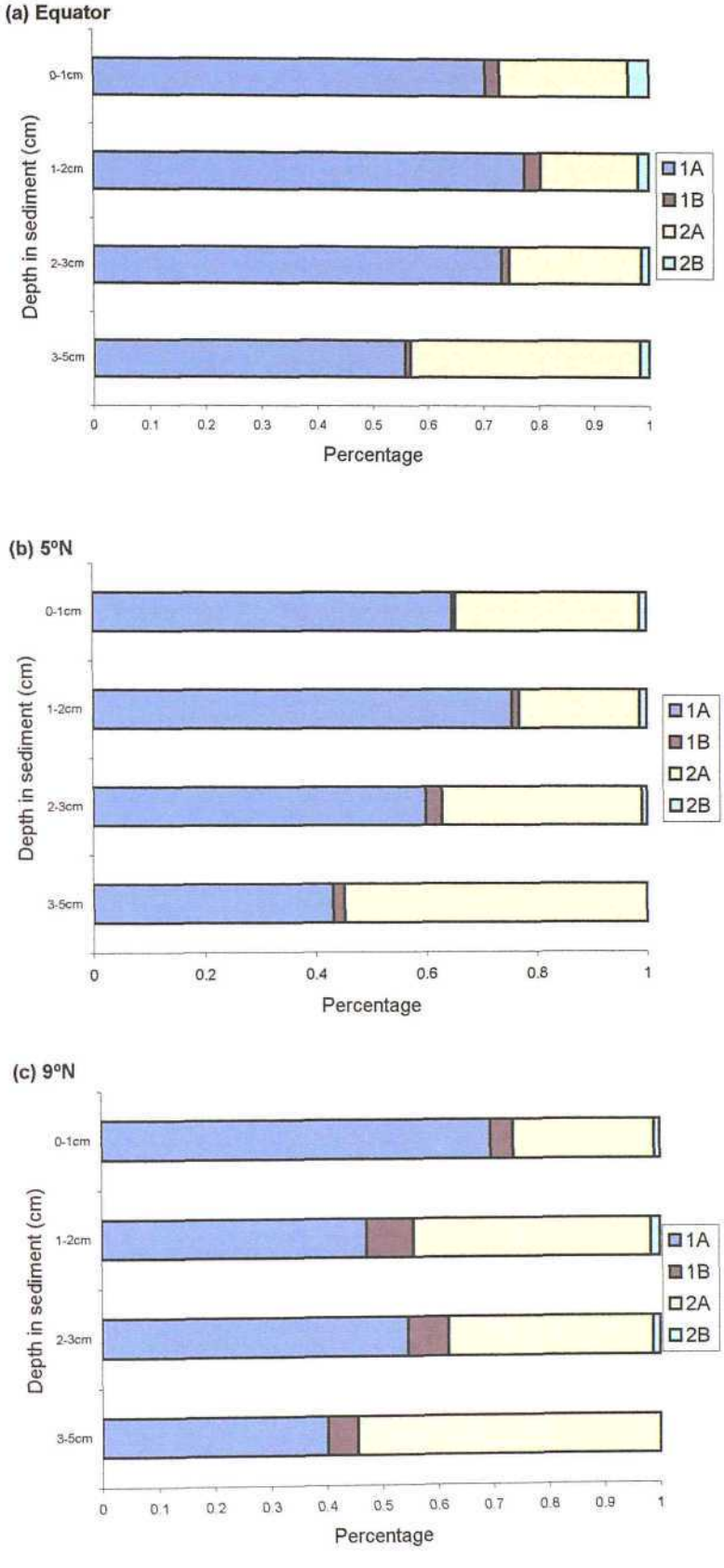


Table 5.2 Species richness within nematode (a) feeding groups and (b) tail-shape groups (richness given as (A) absolute abundance and (B) proportion of total species per sample)

	Equator		2°N		5°N		9°N		23°N	
(a) Feeding group	A	B	A	B	A	B	A	B	A	B
1A	71	58.197	58	59.184	68	60.714	51	57.303	42	51.852
1B	9	7.377	9	9.184	4	3.571	7	7.865	9	11.111
2A	33	27.049	25	25.510	34	30.357	29	32.584	26	32.099
2B	9	7.377	6	6.122	6	5.357	2	2.247	4	4.938
	122		98		112		89		81	
(b) Tail-shape group										
1	2	1.639	2	2.083	2	1.786	2	2.381	1	1.282
2	8	6.557	7	7.292	5	4.464	4	4.762	2	2.564
3	77	63.115	53	55.208	63	56.250	50	59.524	48	61.538
4	35	28.689	34	35.417	42	37.500	28	33.333	27	34.615
	122		96		112		84		78	

Figure 5.2 Nematode feeding-group composition for three stations along the US JGOFS EqPac transect. Vertical profiles for 0-5cm sediment depth. Note that the 3-5cm layer represents a 2cm sediment layer.



A three-way analysis of frequency confirmed a three-way interaction between sediment depth, latitude and feeding group (G-test statistic = 55.136, 18 d.f., $\chi^2_{0.001[18]} = 37.16$, $P < 0.001$). Separate two-way tests of different pairs of variables within a third (Table 5.3) indicated that a highly significant ($P < 0.0005$) association between sediment depth and feeding group is dependent upon latitude. The tests also confirmed the occurrence of greater numbers of type 1B at 9°N and indicated that the relationship between latitude and this feeding type was dependent upon sediment depth.

5.2.2 Horizontal and vertical distribution of tail-shape groups

In the 0-1cm sediment layer, the nematode communities were also dominated by two tail shape groups, (3) conical with a pointed tip and (4) long with tail length greater than five body widths. The conical-type accounted for the greatest percentage of individuals, up to 58.4% at 5°N. There was suggestion of a trend for increasing numbers of tail shape 3 with increasing latitude to 5°N after which the abundance fell. The filiform tail type (4) accounted for a maximum of 47.3% at 9°N. The other two tail-shape groups accounted for less than 5% of the total abundance at all stations. However, within this small percentage that is neither tail-shape group 3 or 4, there was a change from predominately group 2 at the 0-5°N stations to predominately group 1 at the 9-23°N stations (Figure 5.3). A row-by-column analysis of frequency confirmed the heterogeneity of the distribution of individuals among tail-shape groups (G-test statistic = 123.954, d.f. = 12, $\chi^2_{0.001[12]} = 32.91$, $P << 0.001$). The results of subsequent Kruskal-Wallis pair-wise tests (Table 5.4) indicated that the change in the abundance of group 1 was almost significant ($P = 0.079$). No other tail-shape group showed a significant change in abundance with latitude.

Tail-shape groups 3 and 4 were also the most speciose accounting for up to 63.1% and 35.42% of the total number of species per station respectively (Table 5.2). However, there was no general trend connecting tail shape with latitude as was observed in the feeding groups.

Vertically in the sediment a number of patterns with increasing sediment depth were apparent (Figure 5.4). At all stations, tail-shape 4 accounted for the greatest proportion of individuals at nearly all sediment depths, and tail-shape 3 occurred with the second highest

Table 5.3 Mean feeding group trophic composition (± 1s.e.) per station per depth interval with Kruskal Wallis test statistic, Z. (*P** = probability values for the latitude vs. sediment depth analysis)

Equator	1A	1B	2A	2B	Z	*P**
0-1cm	62.667 ± 6.936	2.333 ± 1.333	20.667 ± 3.528	3.333 ± 0.667	0.44	0.881
1-2cm	78.333 ± 0.667	3 ± 1.528	17.667 ± 2.603	2 ± 0.577	-0.17	0.813
2-3cm	67.667 ± 13.836	1.333 ± 0.667	22 ± 4.933	1.333 ± 0.882	-0.34	0.924
3-5cm	54.333 ± 16.677	1 ± 0.577	40.333 ± 16.856	1.667 ± 0.882	0.20	0.901
Z	2.13	-1.59	-2.15	1.83		

5°N	1A	1B	2A	2B	Z
0-1cm	63 ± 8.083	0.667 ± 0.667	32.333 ± 6.984	1.333 ± 0.882	-0.44
1-2cm	75 ± 2.082	1.333 ± 0.333	21.667 ± 2.186	1.333 ± 0.333	-0.45
2-3cm	60.667 ± 1.667	3 ± 1	36.667 ± 3.844	1 ± 0.577	-0.02
3-5cm	34.667 ± 12.238	1.667 ± 0.667	44 ± 21.548	0	-0.45
Z	-0.52	-1.78	1.06	-0.82	

9°N	1A	1B	2A	2B	Z
0-1cm	67.667 ± 5.925	4 ± 1.528	24.667 ± 4.256	1 ± 0	0.00
1-2cm	37.667 ± 15.762	6.667 ± 3.667	34 ± 20.008	1.333 ± 0.333	0.62
2-3cm	55 ± 17.616	7.333 ± 2.728	37 ± 13.748	1.333 ± 0.667	0.35
3-5cm	39.333 ± 8.686	5.333 ± 2.333	53.333 ± 11.695	0	0.25
Z	-1.61	3.37	1.09	-1.01	

	1A	1B	2A	2B	*P*
0-1cm	4.44	-2.98	1.48	-2.94	0.000
1-2cm	4.11	-2.56	1.77	-3.32	0.000
2-3cm	4.07	-2.37	1.84	-3.54	0.000
3-5cm	2.45	-3.82	3.12	-3.82	0.000
P	0.085	0.003	0.100	0.181	

Figure 5.3 Nematode tail-shape group composition for the surface (0-1cm) sediment layer along the EqPac transect. Based on the tail-shape groups of Thistle *et al.* (1995) where type 1 = rounded with blunt end, 2 = clavate-conicocylindrical, 3 = conical and 4 = filamentous.

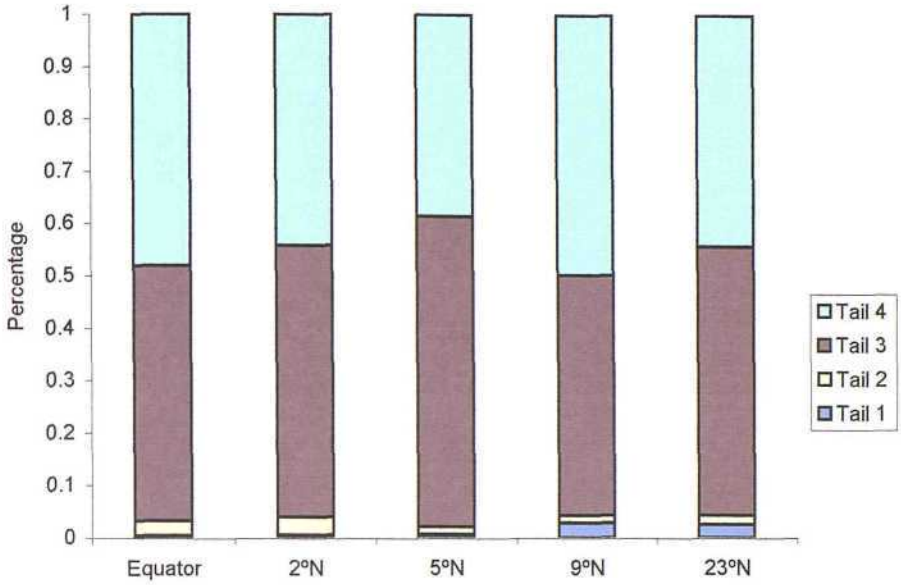
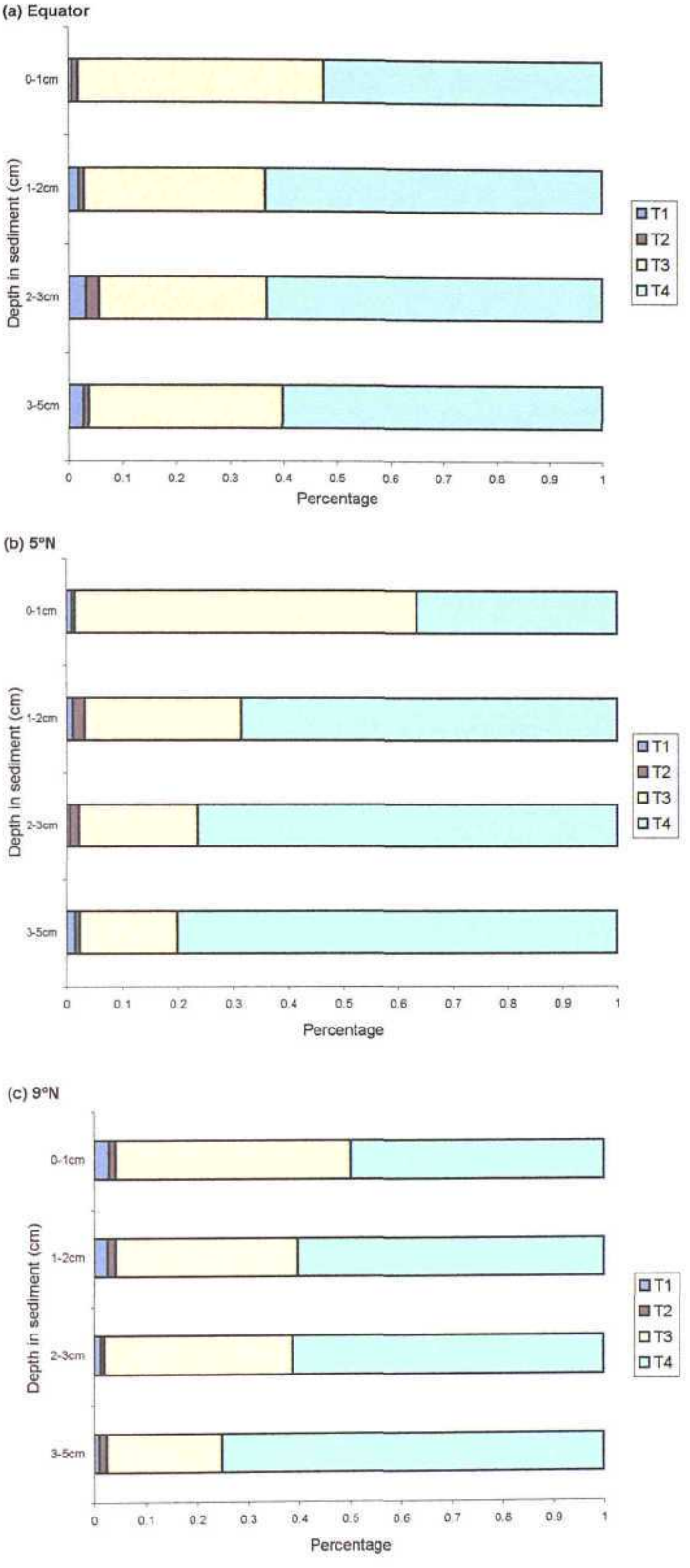


Table 5.4 Mean surface (0-1cm) trophic composition (± 1s.e.) using the tail-shape groups of Thistle *et al* (1995) with Kruskal-Wallis test statistic, Z. (tested for proportional abundance for each trophic group)

	Equator	Z	2°N	Z	5°N	Z	9°N	Z	23°N	Z	*P*
1	0.4 ± 0.4	-1.65	0.5 ± 0.289	-0.81	0.6 ± 0.245	-0.5	2.667 ± 1.202	2.11	2.5 ± 0.957	1.25	0.079
2	2.6 ± 1.030	0.7	3.250 ± 1.109	1.79	1.4 ± 0.748	-1.32	1.333 ± 0.667	-0.4	1.750 ± 0.75	-0.76	0.294
3	45.6 ± 4.250	-1.4	49 ± 3.317	-0.18	58.4 ± 1.030	2.64	43.667 ± 6.064	-0.9	51.750 ± 3.010	-0.36	0.105
4	45 ± 2.387	1.57	41.750 ± 4.956	-0.09	38 ± 1.483	-2.23	47.333 ± 6.692	1.01	44.5 ± 2.901	-0.09	0.162

Figure 5.4 Nematode tail-shape group composition for three stations along the US JGOFS EqPac transect. Vertical profiles for 0-5cm sediment depth. Note that the 3-5cm layer represents a 2cm sediment layer.



frequency. At the equatorial station there was suggestion of a sub-surface maximum in the abundance of tail-shape 4 that occurred between 1 and 3cm sediment depth. The increase in tail-shape 4 corresponded to a decrease in tail-shape 3 and vice versa. However, at stations 5 and 9°N, the occurrence of tail-shape 4 increased with sediment depth, almost exponentially at 5°N and linearly at 9°N (Figure 5.4). At stations 0 and 5°N tail-shapes 1 and 2 exhibited sub-surface maxima in the 2-3 cm and 1-2 cm layers respectively whereas the maxima occurred in the surface 0-1cm layer at 9°N. A three-way analysis of frequency confirmed a very strong interdependence between tail-shape, sediment depth and latitude (G-test statistic = 120.738, d.f. = 18, $\chi^2_{0.001[18]} = 37.16$, $P << 0.001$). Subsequent pair-wise analyses with a Kruskal-Wallis test of the proportion of individuals per tail-shape group (Table 5.5) indicated a highly significant change in tail-shape group with sediment depth ($P < 0.0005$), that was correlated with latitude.

5.2.3 Combined feeding and tail-shape functional group approach

Each feeding-group-tail-shape group combination was treated as an *operational classificatory unit* (OCU) and the resulting OCU lists for the 0-1cm sediment layer at each station were subjected to cluster analysis using the Bray-Curtis index of similarity with subsequent double-root ($\sqrt{\sqrt{}}$) -transformation of the data. Contrary to expectations, the combined functional groups did not separate out to any recognisable pattern (Figure 5.5a) for the 0-1cm sediment layer and similarity was greater than 82%. Little grouping was discernible either by station or by sampling method. This last point is reassuring as it strengthens the decision to collate the data by station, regardless of sampling strategy. However, given the significant relationships that were recorded independently for feeding groups and tail-shape groups with changing latitude, the almost complete absence of any notable similarity in the combined functional-group approach is somewhat surprising. $\sqrt{\sqrt{}}$ -transformation of the data prior to cluster analysis did not assist in separating the samples any more adequately (Figure 5.5b). The absence of any clustering patterns was demonstrated in an area plot of the percentage of individuals for each OCU for each sample along the latitudinal transect (Figure 5.6). Whilst it is understood that it is incorrect to display discrete samples as a continuous plot, it provides an 'at-a-glance' picture of the distribution of individuals among OCUs.

Table 5.5 Mean tail shape trophic compostion (± 1s.e.) per station per depth interval with Kruskal-Wallis test statistic, Z. ($P*$ = probability values for latitude vs. sediment depth analysis)

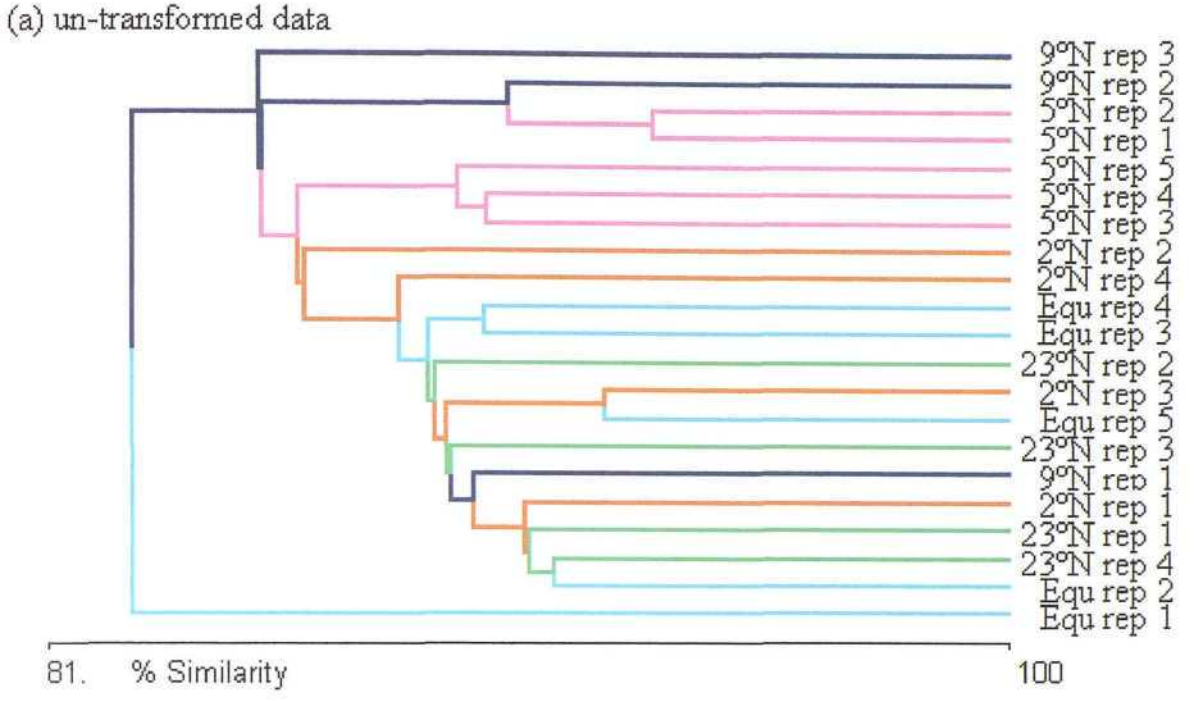
Equator	1	2	3	4	Z	$P*$
0-1cm	0.667 ± 0.667	1 ± 0	40.667 ± 5.457	46.667 ± 3.930	-0.18	0.878
1-2cm	2 ± 0.557	1 ± 0.577	34 ± 8.145	64 ± 7.371	-0.05	0.993
2-3cm	3 ± 2.082	2.333 ± 1.856	28.667 ± 6.936	58.333 ± 2.404	0.3	0.946
3-5cm	2.667 ± 0.333	1 ± 1	35 ± 16.523	58.667 ± 18.523	0.30	0.941
Z	0.82	-0.17	0.87	-0.54		

5°N	1	2	3	4	Z
0-1cm	1 ± 0	0.667 ± 0.667	60 ± 1.155	35.667 ± 0.667	-0.32
1-2cm	1.333 ± 0.882	2 ± 0.577	28 ± 4.726	68 ± 5.292	0.12
2-3cm	0.667 ± 0.333	1.667 ± 1.202	21.667 ± 4.631	77.667 ± 7.311	-0.27
3-5cm	1.333 ± 0.882	0.667 ± 0.667	14 ± 7.024	64 ± 15.75	-0.03
Z	-1.43	0.1	-1.04	1.04	

9°N	1	2	3	4	Z
0-1cm	2.667 ± 1.202	1.333 ± 0.667	43.667 ± 6.064	47.667 ± 6.386	0.50
1-2cm	2 ± 0.577	1.333 ± 1.333	28.333 ± 11.465	48 ± 19.655	-0.07
2-3cm	1.333 ± 0.667	0.667 ± 0.333	37 ± 7.024	61.667 ± 4.631	-0.03
3-5cm	1 ± 0.577	1.333 ± 0.882	22 ± 4.163	73.333 ± 7.535	0
Z	0.6	0.07	0.17	-0.5	

Z	1	2	3	4	P
0-1cm	-2.96	-2.96	3.14	2.78	0.000
1-2cm	-2.61	-3.31	1.92	4	0.000
2-3cm	-2.87	-3.05	1.48	4.44	0.000
3-5cm	-2.45	-3.47	1.63	4.29	0.000
P	0.355	0.536	0.536	0.582	

Figure 5.5 Cluster analysis of combined two-way functional groups for the surface (0-1cm) sediment layer using the Bray-Curtis index of similarity (single link). Dendograms shown for (a) original data and (b) double-root (√√) -transformed data.



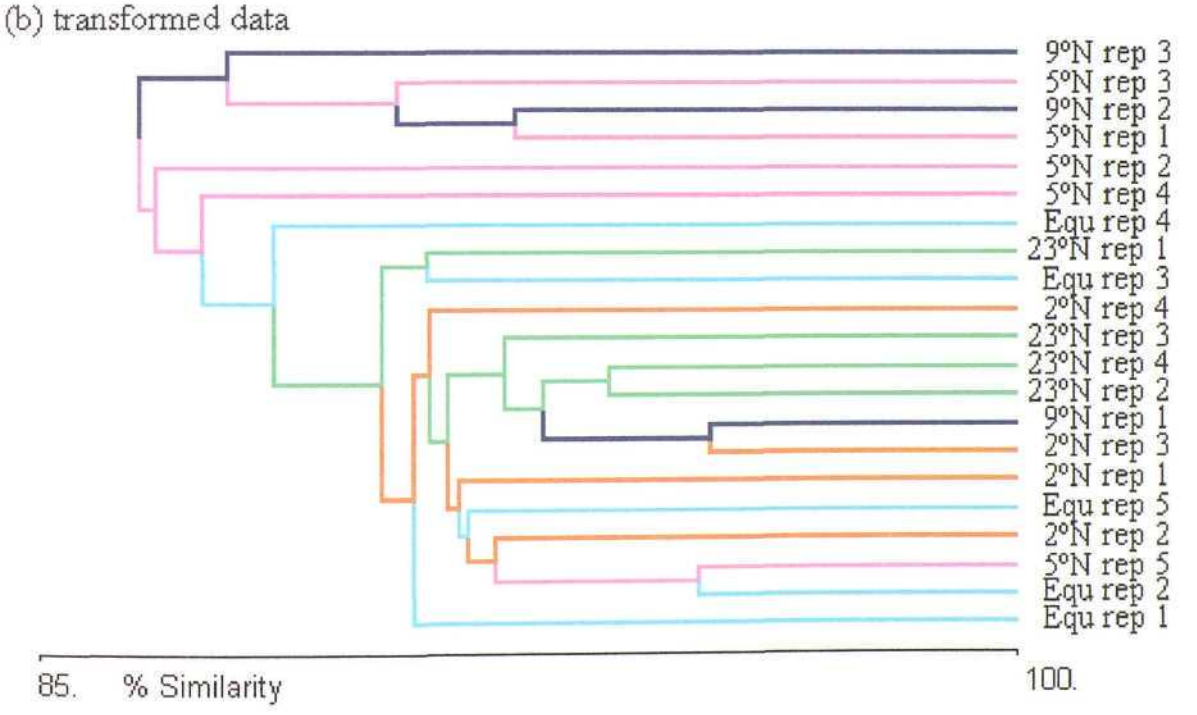
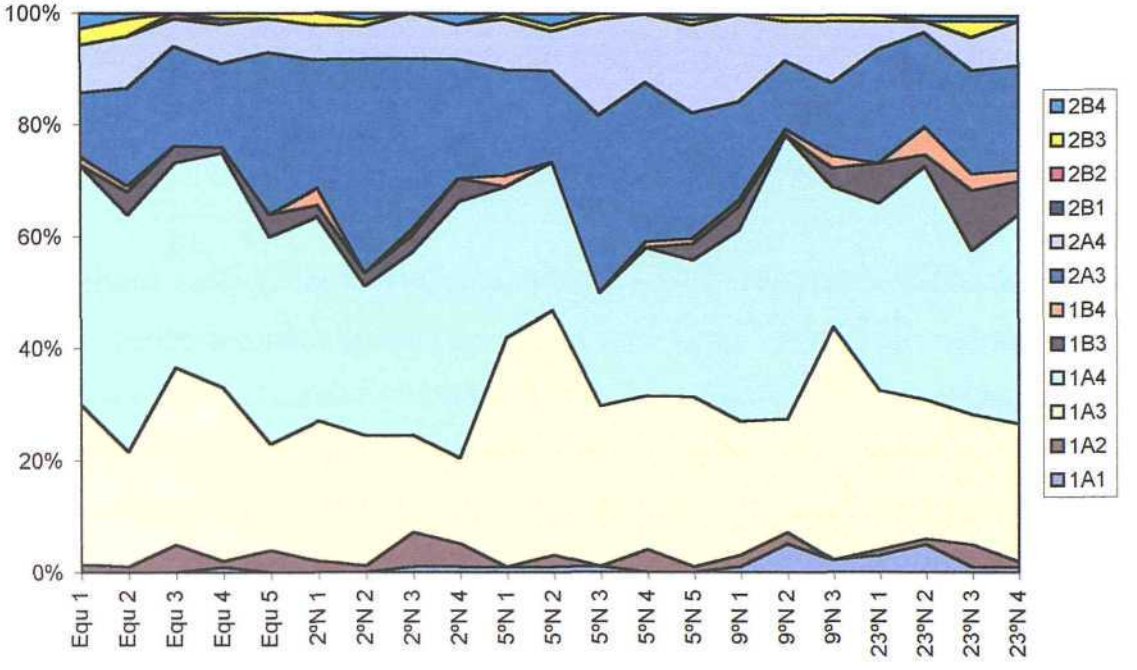


Figure 5.6 Area plot of combined two-way functional groups as percentage of individuals per sample, for the surface (0-1cm) sediment layer for each station along the US JGOFS transect.



An area plot was also constructed for vertical profiles of the OCU lists at each latitude, for each sediment horizon (Figure 5.7). Overall, there was evidence of change in the dominance of particular groups with depth in the sediment. Group 2A4 (epistrate feeders with filiform tail) increased in numbers with increasing sediment depth and this corresponded to a decrease in numbers of groups 1A3 (selective deposit feeders with conical tail) and 2A3 (epistrate feeders with conical tail). Group 1A4 (selective deposit feeders with filiform tail) appeared to occur most frequently between 1 and 3cm sediment depth. No pattern of change with latitude was discernible, however.

When cluster analyses for the vertical profiles at each station were examined, there was little separation according to sediment depth (Figure 5.8a). At 5°N there was some clustering of the surface (0-1 cm) samples apart from the other sediment layers but there was little evidence of further clustering deeper in the sediment. At 0 and 9°N clustering by sediment depth was not obvious. Once again, similarity between samples is particularly high (greater than 70%) and separation does not appear to follow any predictable pattern. Furthermore, $\sqrt{\sqrt{}}$ -transformation prior to cluster analysis was unhelpful (Figure 5.8b).

Clustering was more defined when the samples were pooled according to latitude and the same sediment layers were compared (Figure 5.9). The 0-1cm sediment layer did not show particularly good separation, but this improved in the 1-2 cm sediment layer where samples from 0 and 5°N were clustered together and samples from 9°N fell together, although similarity for the two groups was 74%. Likewise, there was good clustering of the 0 and 5°N samples from the 2-3 cm layer, with the 9°N samples falling in a separate group (65% similarity for un-transformed data and 82% similarity for $\sqrt{\sqrt{}}$ -transformed data). However, in the 3-5cm sediment layers clustering was less well-defined with some overlap between all three stations.

Figure 5.7 Area plot of combined two-way functional groups as percentage of individuals per sample for three stations along the US JGOFS transect from four sediment depths.

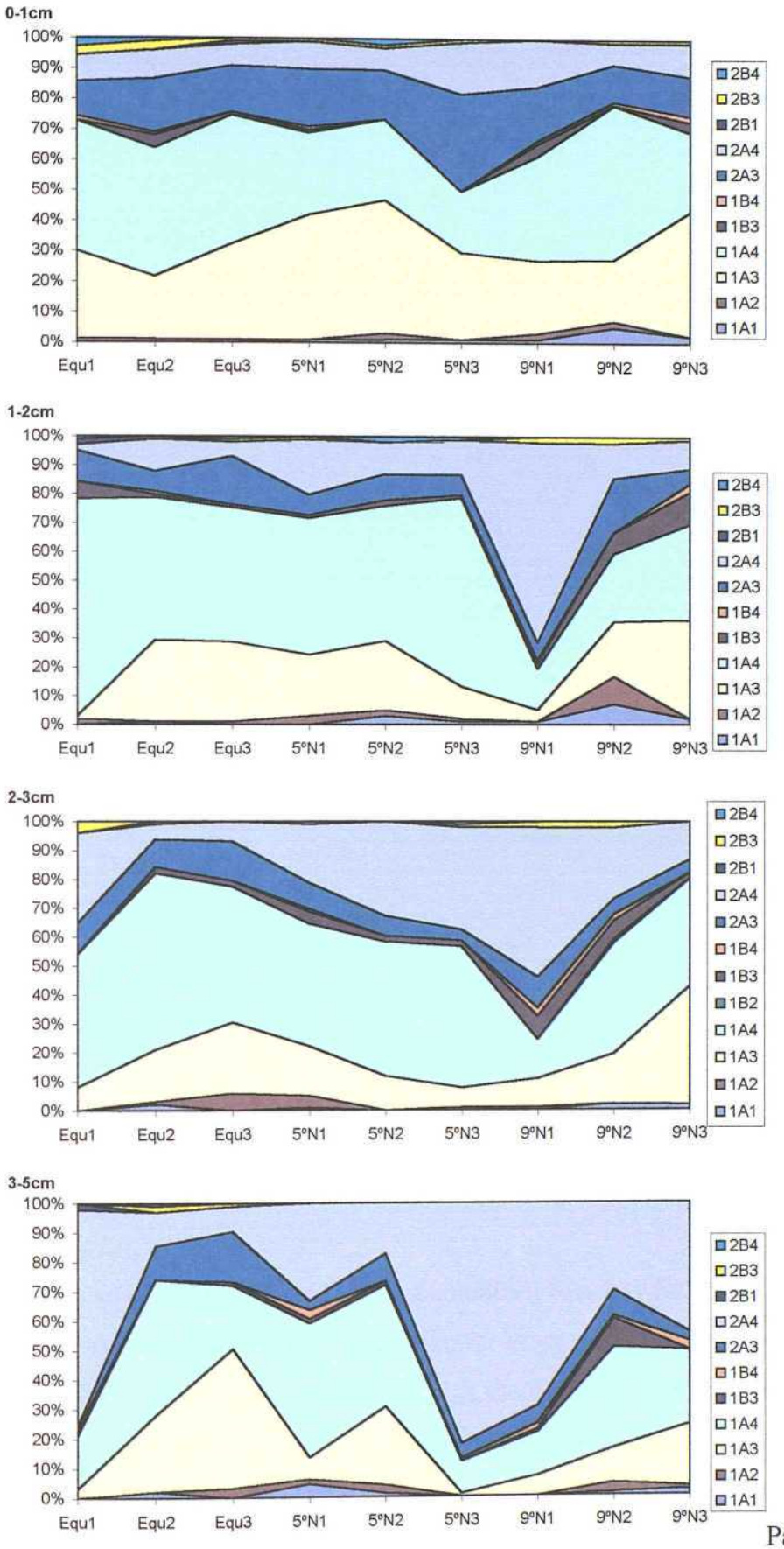
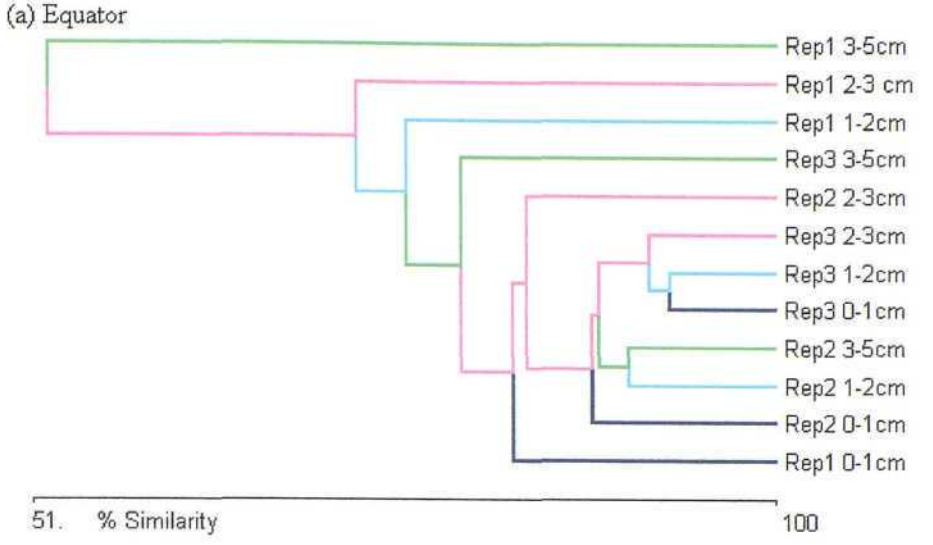
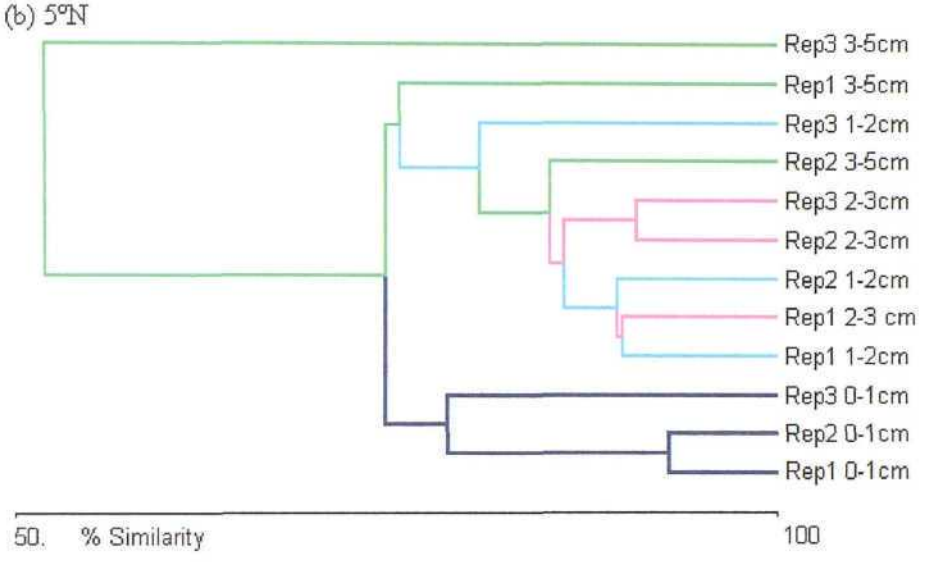
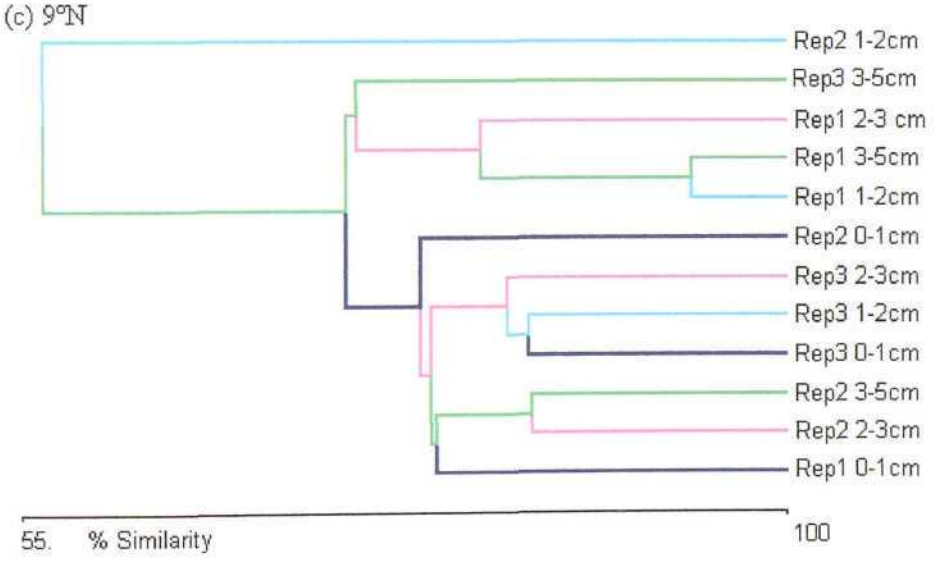


Figure 5.8 (shown overleaf) Cluster analysis of combined two-way functional groups for three stations along the EqPac transect. Clustering for original data for three replicate samples from four sediment depths are shown using the Bray-Curtis index of similarity (single link) for (a) untransformed data and (b) √√- transformed data.

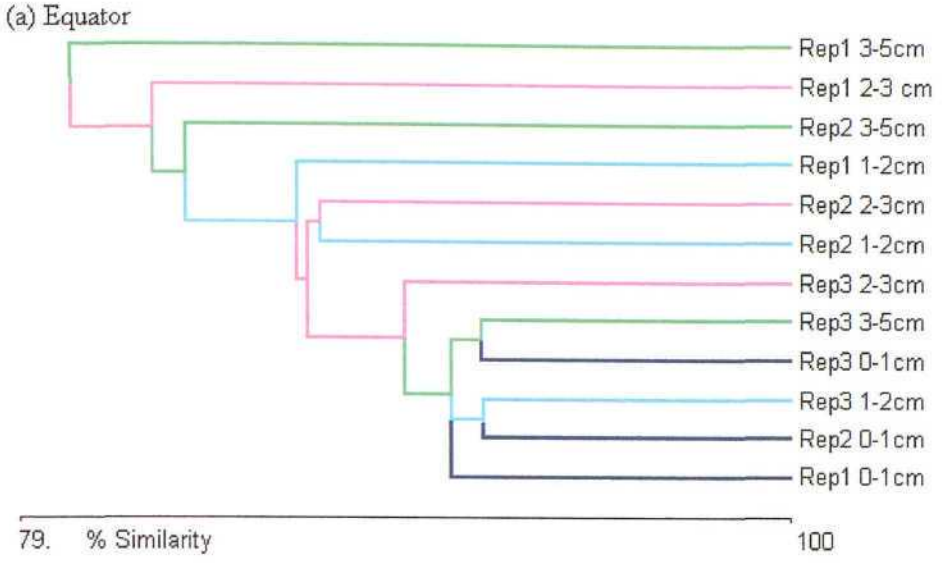
(a) untransformed data

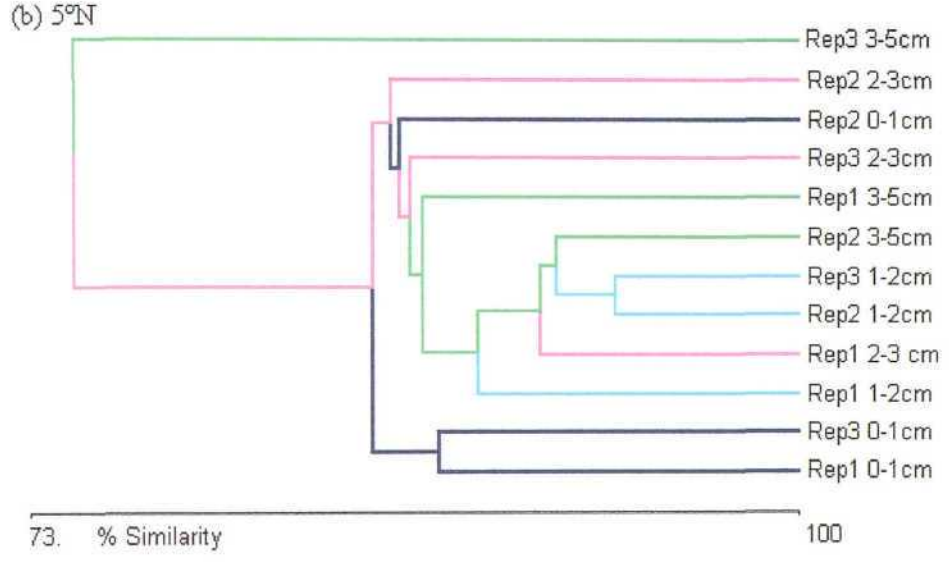






(b) √√-transformed data





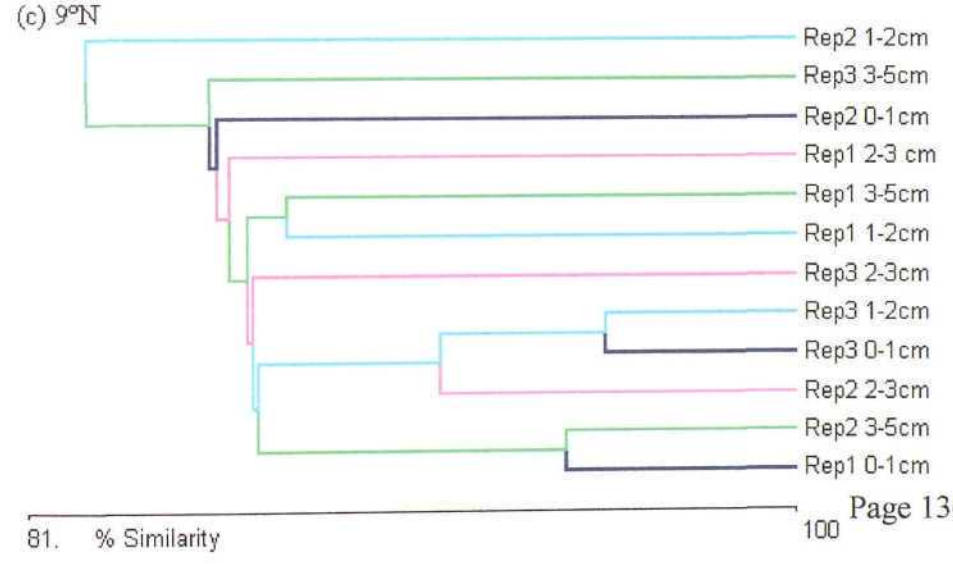
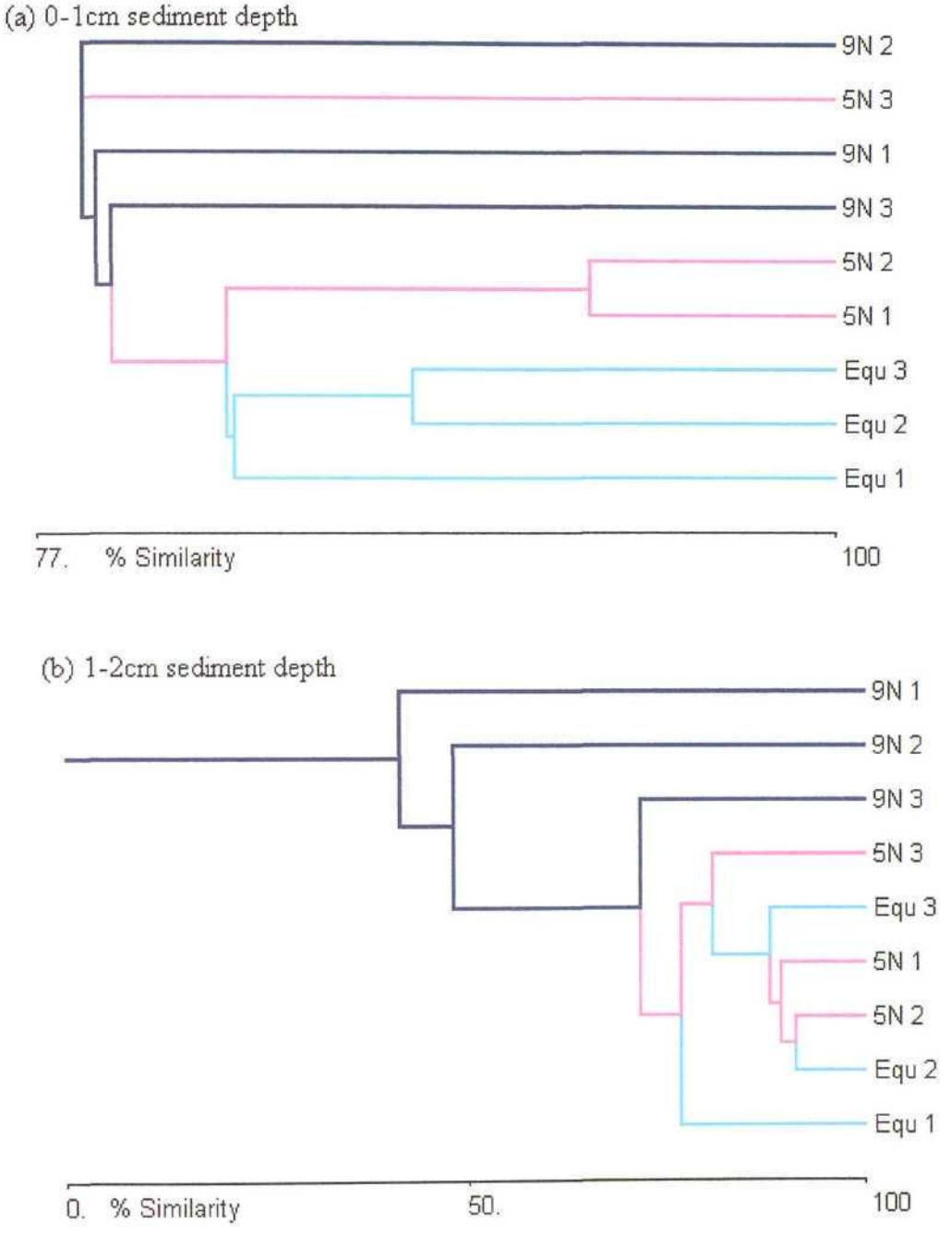
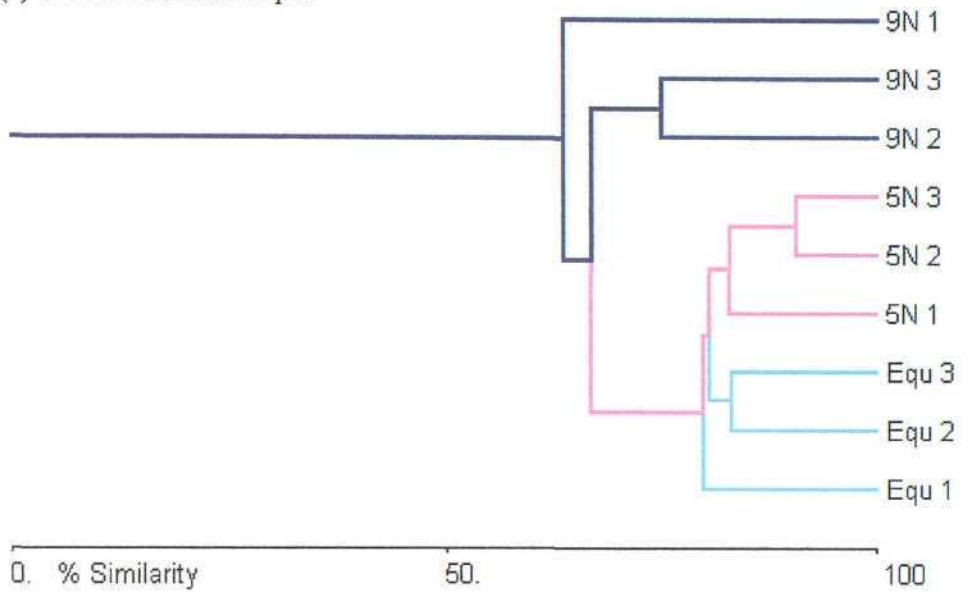


Figure 5.9 Cluster analysis of combined two-way functional groups for three stations along the EqPac transect. Data are shown for three replicates from each station per sediment layer using the Bray-Curtis index of similarity (single link) for (a) untransformed data.



(c) 2-3cm sediment depth



(d) 3-5cm sediment depth

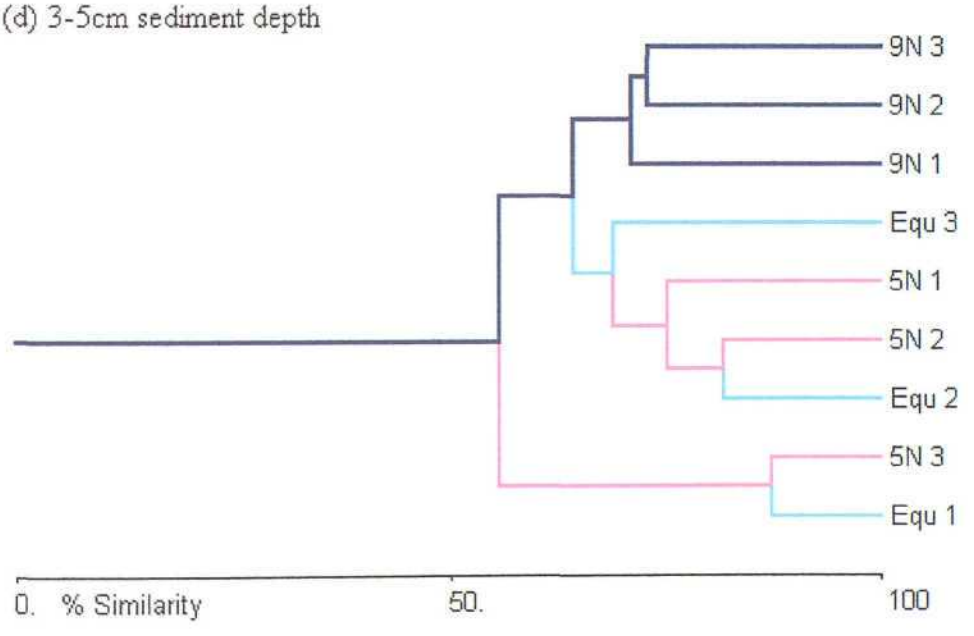
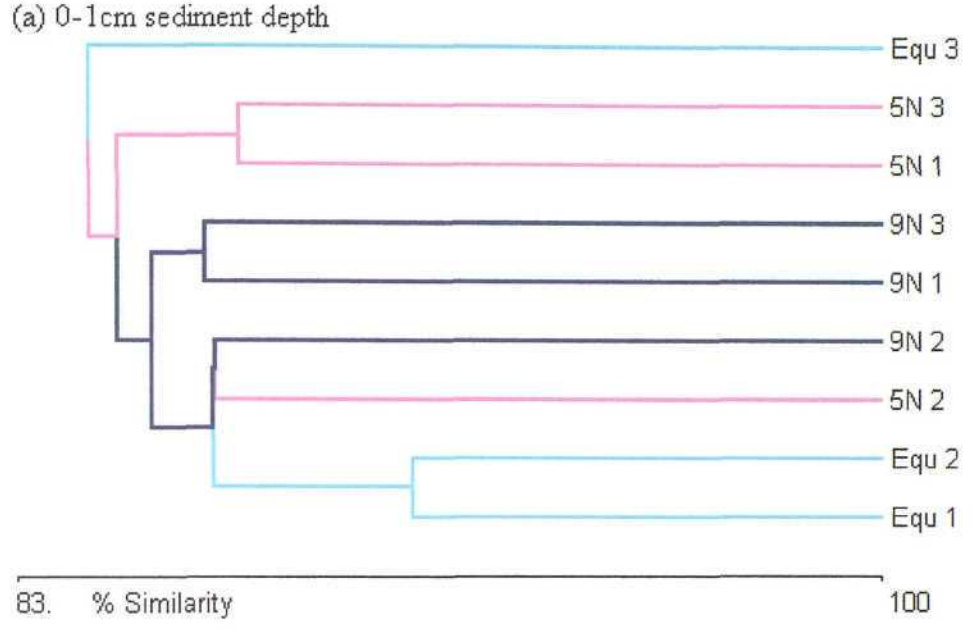
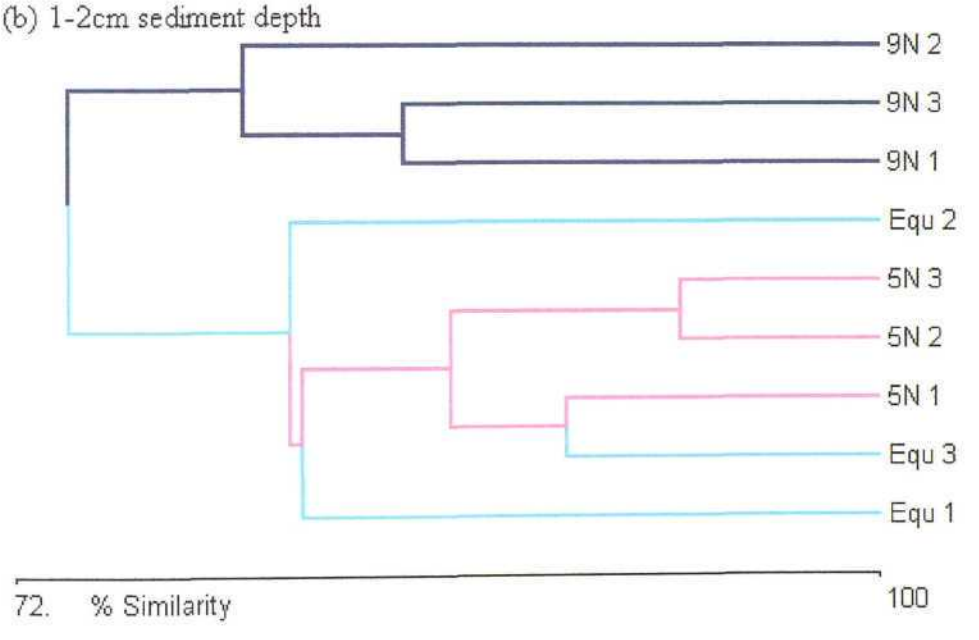
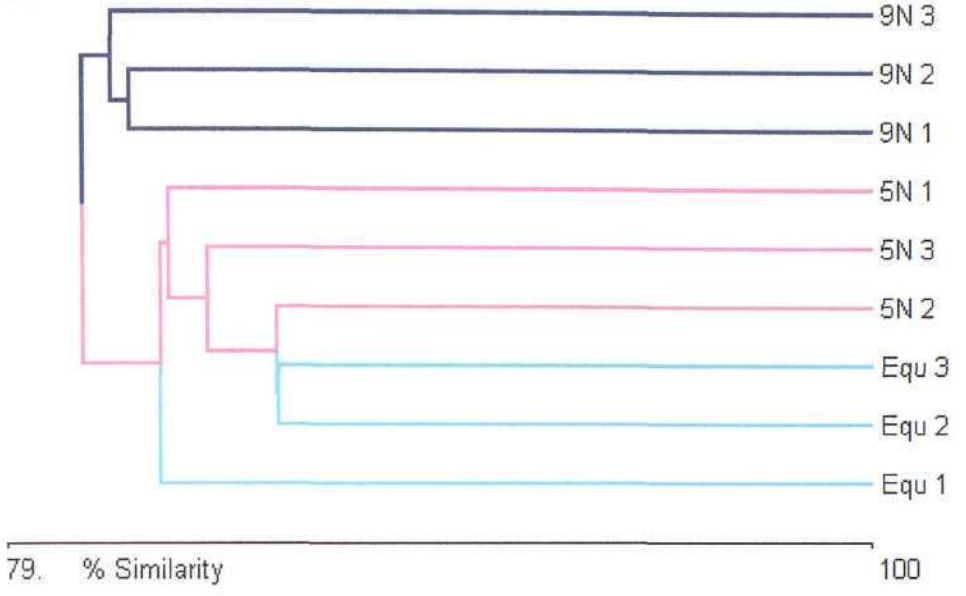


Figure 5.9 cont'd. (b) √√- transformed data.

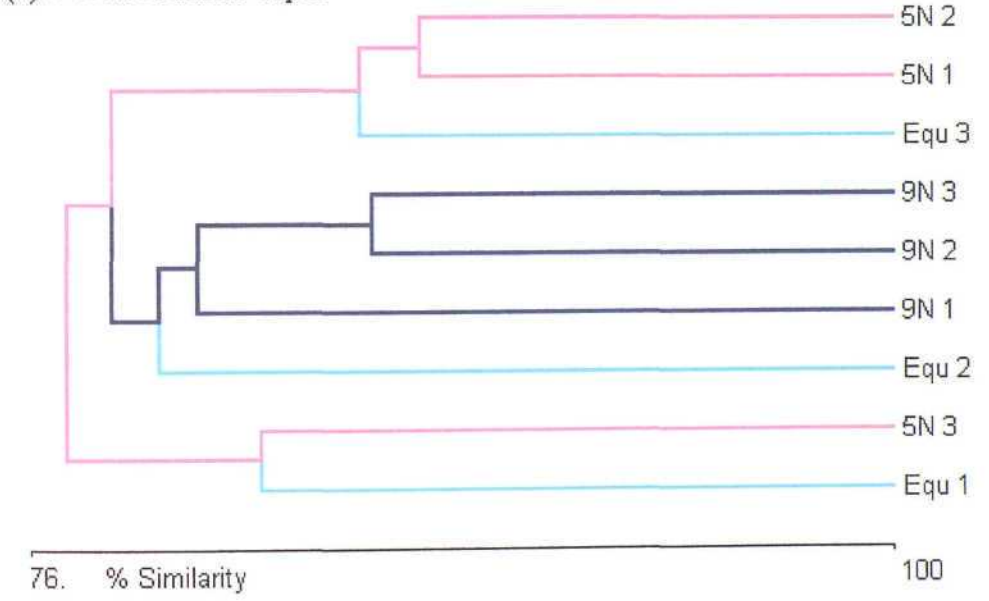




(c) 2-3cm sediment depth



(d) 3-5cm sediment depth



5.3 Discussion

The nematode assemblages of the central equatorial Pacific were strongly dominated by deposit feeders. This is concordant with other studies of the trophic composition of deep-sea nematode communities. The combined 1A and 1B groups accounted for between 59 and 76% of all individuals and between 53 and 68% of all species analysed from these sites in the 0-1cm sediment layer. In samples collected from the Porcupine Abyssal Plain (NE Atlantic) which also receives a substantial, seasonal input of phytodetritus, 50-70% of the nematodes belonged to either the 1A or 1B feeding type (Thistle *et al.*, 1995). Similarly, at the DORA site, also in the NE Atlantic, deposit feeders predominated (Rutgers van der Loeff and Lavaleye, 1986). Within the deposit feeders, the reported distribution of individuals between selective (1A) and non-selective (1B) strategies varies considerably. For example, Thistle and Sherman (1985) reported dominance by 1Bs at the HEBBLE site in the NW Atlantic, and similarly from the Venezuela Basin (Tietjen, 1984). Studies at the Porcupine Abyssal Plain and also at the Madeira Abyssal Plain cite 1As as the dominant trophic group (Thistle *et al.*, 1995) and at the DORA site, 1As and 1Bs were almost equally represented (Rutgers van der Loeff and Lavaleye, 1986). In the equatorial Pacific, 1Bs accounted for between 1.4 and 9.25% of total number of individuals in the samples compared with compared with 56.5 – 68% that were 1As.

This pattern may be due to different approaches in the use of Weiser's (1953) classification. Earlier authors often followed the list of genera that Wieser had assigned to particular feeding groups in his paper, without consideration of the actual buccal morphology. For example, the supragenus *Monhystera* (c.f *Thalassomonhystera*) was assigned to the 1B feeding group by Wieser (1953), whereas later authors (Thistle & Sherman, 1985; Thistle *et al.*, 1995) placed individuals in the 1A category, based upon the size of the buccal cavity. This latter approach is the method followed in the present study, but it does present problems when comparing the results with those of earlier studies. However, the discrepancy in contributions made by the 1B and 1A feeding groups, in all studies, did appear to correspond well to organic input. The percentage of 1Bs increased significantly with increasing latitude along the JGOFS EqPac transect, as organic flux to the seafloor decreased (Honjo *et al.*, 1995). Similarly, the organic input to the Porcupine Abyssal Plain was greater than in the Venezuela Basin (Tietjen, 1984) and at the DORA

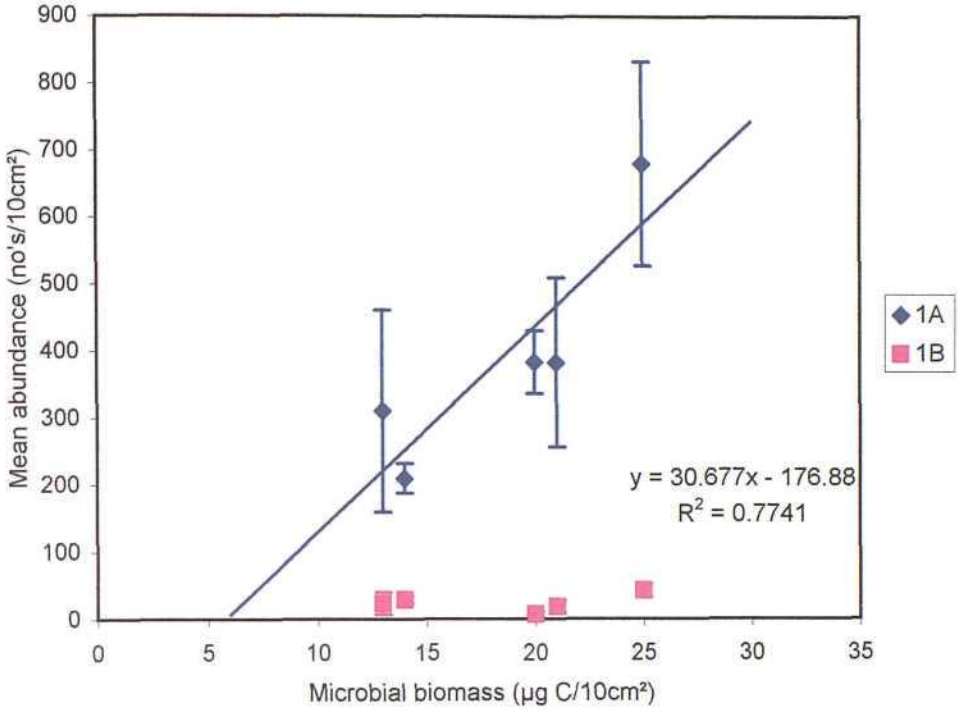
station (Rutgers van der Loeff and Lavaleye, 1986). However, the HEBBLE site on the Scotian Rise also receives a elevated input of organic material compared to the majority of abyssal sediments and yet 1B appeared to be the predominate feeding type (Thistle and Sherman, 1985). Thistle *et al.* (1995) proposed that this could be attributable to the vigorous hydrodynamic regime experienced at this location. They argued that the frequent benthic storms that scour the surface sediments may wash away many of the smaller particles that 1A nematodes feed on.

Observations of estuarine 1A nematodes suggest that they feed primarily on bacteria, by means of continuous oesophageal contractions that pump material into the buccal cavity (Romeyn and Bouwman, 1983). Selectivity can be passive, in that particles must be small enough to enter the tiny buccal cavity, or alternatively individual bacteria can be actively chosen. Additionally, studies have demonstrated that variations in shallow-water nematode densities are directly related to the varying size of bacterial populations (Boucher and Chamroux, 1976; Trotter and Webster, 1984). In the equatorial Pacific, analyses of phytodetrital material have demonstrated the presence of a metabolically-active microbial population (Smith *et al.*, 1996) and similarly, elevated bacterial numbers have been recorded from the sediments in areas receiving a high phytodetrital flux (Dobbs, *in prep.*). Consequently it would seem reasonable to suppose that the high availability of food for 1A nematodes is responsible for their disproportionate representation.

There was a significant, positive correlation between the abundance of individuals in the 1A and 1B feeding groups, and microbial biomass ($r = 0.880$, $P < 0.025$), in agreement with this suggestion (Figure 5.10). The absence of a significant correlation between the abundance of 1B nematodes and microbial biomass may be explained by the more general feeding behaviour of this trophic group, which has been reported to select protozoa and small ciliates in addition to bacteria (Alongi and Tietjen, 1980; Romeyn and Bouwman, 1983; Jensen, 1987).

It would be expected that dependence upon the microbial communities of the sediments, as opposed to a phytodetrital community, would increase with increasing latitude as the phytodetrital input decreased. This is supported, in part, by the significantly greater proportions of non-selective deposit feeders that make up the nematode communities at 9

Figure 5.10 Abundance of 1A and 1B nematodes correlated with microbial biomass for 0-1cm sediment layer. Microbial biomass values are taken from Smith *et al.* (1997). Error bars are ± 1s.e. Regression line equations are shown on the chart.



and 23°N. The trophic shift towards a more catholic diet may offer a means of meeting energetic requirements under resource-limited conditions. This is in direct contradiction of competitive equilibrium theories, which would predict that species would become more specialised as food availability becomes increasingly restricted (see Chapter 2). The nematode communities appear to be structured by variables other than competition, in agreement with Connell's (1978) Intermediate Disturbance Hypothesis. However, it is important to note that feeding groups oversimplify trophic interactions within the nematode communities and such patterns may be artefacts of this arbitrary grouping.

The vertical profiles of trophic composition indicate a subsurface maximum in the 1-2cm sediment layer at 0 and 5°N in the proportional abundance of 1A nematodes. Unfortunately no published data on the vertical distribution of microbial biomass are available for the EqPac stations so it is impossible to state whether microbial biomass might also be disproportionately represented in the 1-2cm sediment layer. However, vertical profiles of chlorophyll *a* and ^{234}Th, which are considered to be good proxies for labile organic carbon (Stephens *et al.*, 1997) do display subsurface maxima due to bioturbation activity by megafaunal animals, such as mobile urchins, which are more abundant at the 0-5°N stations (Hoover, 1995). There was no evidence for disproportionate representation of 1A nematodes below the 0-1cm sediment layer at the 9°N station. This suggests that there may indeed be a subsurface microbial biomass maximum that is responsible for the disproportionate representation of 1A nematodes below the surface layer at 0 and 5°N.

The high proportions of epistrate (2A) feeders that were recorded from the EqPac stations are also characteristic of areas receiving a significant input of phytodetrital material. At the Porcupine Abyssal Plain station (NE Atlantic), 2A nematodes were the second most important feeding group after deposit feeders (Thistle *et al.*, 1995), and also at the HEBBLE site in the NW Atlantic (Thistle and Sherman, 1985). Similarly, in addition to high numbers of monhysterid nematodes, Thiel *et al.* (1988/89) also commented on the occurrence of chromadorid nematodes within the phytodetrital aggregates collected from the BIOTRANS site in the NE Atlantic. Chromadorids are characterised by the presence of a medium-sized buccal cavity with one or more small teeth, i.e., they generally fall in Wieser's (1953) 2A feeding group. Data from the Madeira Abyssal Plain (NE Atlantic) are

in agreement with this observation. MAP is noted for a relatively high organic carbon flux, but absence of a phytodetrital input that would supply intact diatoms (Honjo and Manganini, 1993). Correspondingly, 1A nematodes were dominant, but there were substantially fewer 2A feeding type individuals (20%) when compared with PAP (39%) that does receive a phytodetrital input (Thistle *et al.*, 1995).

Romeyn and Bouwman (1983) describe three *modi operandi* for epistrate feeders: *piercing*, where the nematode first punctures the cell before swallowing the liquid contents; *cracking*, when the nematode crushes the cell to fracture the wall before, again, swallowing the contents; and swallowing the cell intact. A number of observations of shallow-water epistrate feeders have confirmed these feeding methods (Jensen, 1983; Romeyn and Bouwman, 1983; Trotter and Webster, 1984; Jensen, 1987). Experimental evidence has confirmed a high degree of discrimination by the nematode, between bacteria and unicellular algae, and within each food type, selection for the right-sized particle for ingestion (Tietjen and Lee, 1977; Alongi and Tietjen, 1980; Trotter and Webster, 1984). Whilst no observations have been made of the feeding ecology of nematodes of the equatorial Pacific, it would seem reasonable to imply similar feeding mechanisms for these 2A nematodes.

Analysis of the composition of phytodetrital material found in aggregates at the 0-5°N stations (Smith *et al.*, 1996) indicated the presence of intact pennate and centric diatom cells as well as large numbers of miscellaneous microalgae. Smith *et al.* (1996) also reported that coverage of the sediments by phytodetrital material was greatest at the equatorial station and decreased with increasing latitude. Greatest numbers of epistrate feeders would therefore be expected to occur at the equator. In contrast to this expectation, greatest densities of epistrate feeders were recorded from 5°N. However, remembering the high correlation between nematode biomass and POC flux averaged over the five months prior to the benthic sampling event (Chapter 4, section 4.3), the high proportion of 2A nematodes at 5°N correlates well to the greater flux of particulate organic carbon material that was hypothesised to have arrived at the seafloor during this period, compared with the equatorial station, i.e. it is a relict fauna. The occurrence of greater proportions of 2A nematodes from sites in the NE Atlantic reported to receive a phytodetrital input appear to agree with this hypothesis (Thistle and Sherman, 1985; Thiel *et al.*, 1988/89; Thistle *et al.*,

1995). Further evidence in support of this hypothesis includes observations of the presence of diatom remains in the guts of 2A nematodes from stations at 0-5°N.

In a study of deep-sea nematode assemblages of the Venezuela Basin, Tietjen (1984) also found a high correlation between the abundance ratio of epistrate feeders (2A) to deposit feeders (1A/B) and sediment type. 2As were more abundant in heterogeneous pelagic sands than in homogeneous hemipelagic and turbidite muds. Tietjen (1984; 1989) inferred that the poor sorting of the pelagic sediments and larger median grain size permitted a larger and more varied community of 2As to co-exist. Tiejen (1984) suggested that this was because epistrate feeders can rasp organic particles off large sand grains with their teeth, whereas deposit feeders are restricted to ingestion of bacteria or small mud particles. Although there is a noticeable change in sediment composition between 5 and 9°N from predominately calcareous foraminiferal muds to fine-grained clays (Berelson *et al.,* 1994; Stephens *et al.*, 1997), there was no significant drop in the relative abundance of epistrate feeders with a corresponding increase in deposit feeders at these latitudes. Consequently, the change in sediment type does not appear to be responsible for structuring the trophic composition of EqPac nematodes.

Additionally, no significant change in sediment composition was recorded between the sediment surface and 5cm depth, yet a marked change occurs in the relative proportion of epistrate feeders to deposit feeders. At 0 and 5°N the abundance of epistrate feeders was initially high at the surface, before dropping to minimal values in the 1-2cm sediment layer. Subsequently, they attained maximum values in the 3-5cm sediment layer and were the dominant trophic group at these depths. The ecological explanation for the increased occurrence at these greater depths is unknown, but it must be a common factor at all three EqPac stations. As the occurrence of intact algal cells was reported to be very rare at the 9°N station (Smith *et al.*, 1996), it must be assumed that the epistrate feeders were utilising alternate food resources not dependent upon a fresh supply of phytodetritus. Previous studies have demonstrated the importance of bacterial gardening in a number of nematode species (Riemann and Schrage, 1978; Jensen, 1987) and uptake of dissolved organic material is also thought to be important in some species (Chia and Warwick, 1969; Lopez *et al.*, 1979; Riemann *et al.*, 1990), including some 2A-type nematodes. It is

possible that such feeding modes increase in importance with a decrease in the supply of surface-derived, labile, particulate organic material.

The occurrence of predatory or scavenging nematodes was very rare in equatorial Pacific nematode communities, accounting for less than 10% of the total number of individuals at each station. This is a feature common to many of the deep-sea nematode communities that have been studied (Tietjen, 1984; Rutgers van der Loeff and Lavaleye, 1986; Jensen, 1988; Tietjen, 1989; Thistle *et al.*, 1995). Jensen (1988) attributed the low densities of scavengers to a lack of freshly dead organisms, as biomass in the deep sea is generally low and most species are long-lived. Similarly, in a deep-sea canyon in the Mediterranean, a high input of organic matter to the canyon floor was said to permit a greater trophic complexity which, in turn, corresponded to elevated numbers of predatory nematodes (Soetaert and Heip, 1995). It seems likely, therefore, that the slight increase in numbers of 2B-type nematodes at the equatorial EqPac station may be due to the increased carbon input to the sediments and prey densities. This postulation is supported by the greatest proportion of 2B-type nematodes occurring in the 0-1 cm sediment layer and decreasing in numbers with depth vertically in the sediment. Unlike the smaller, bactiverous nematodes which are thought to respond to organic input on a very short time-scale, shallow-water predatory nematodes have much longer generation times, with perhaps only one generation annually (see review in Heip *et al.*, 1985). In the deep sea, where metabolic activity is generally slower (Gage and Tyler, 1991), similar response times are predicted. Consequently, as for the macrofauna (Smith *et al.*, 1996), it is expected that the distribution of these longer-lived species would correlate best with an annual POC flux value (Honjo *et al.*, 1995) and indeed this appears to be the case.

It was noted that the 2A feeding type occurred most frequently with tail shape 3 (conical) in all of the 0-1cm sediment samples, in terms of total individuals. There are two possible explanations for this co-occurrence. Firstly, that historically the two morphologies evolved together and subsequent radiation of species with this buccal morphology has not required any alteration in tail structure. Alternatively, this particular tail shape may be advantageous in some way to species feeding in this manner and was selected for during speciation.

The functional significance of only one of the four tail-shape groups of Thistle *et al.* (1995) is known, based on Riemann's (1974) observation that long-tailed (type 4) nematodes were hemi-sessile, spending substantial periods attached to the substratum by means of the caudal-gland adhesive secretions. Riemann (1974) also observed that the individual anchored the tail tip to the substratum and then moved away from the anchor point, extending the long tail. When necessary, the tail could be tightly coiled to pull the nematode quickly back to the anchor point. Ax (1963) considered this type of tail morphology to be typical of inhabitants of the interstitial spaces in sand and Thistle *et al.* (1985) suggested that the hemi-sessile function was advantageous in the vigorous hydrodynamic regime of the HEBBLE site in the NW Atlantic by aiding avoidance of re-suspension during the sub-catastrophic benthic storm events that frequent the area. Riemann (1974) suggested that this tail shape was an adaptation to fine sediments and flocculated masses of detritus, where the interstices do not necessarily interconnect and are too narrow to permit the nematode to bend backwards and escape.

It is possible that along the EqPac transect, the functional advantage of the long tail-shape concerns moving within phytodetrital aggregates according to Riemann's (1974) hypothesis. Tail-shape groups 3 and 4 dominated the nematode communities at all stations along the EqPac transect and at all depths within the sediments. However, the absence of a clear correlation of any tail-shape group with POC flux would suggest that elevated POC flux does not influence tail shape, as it does feeding type. If tail shape does play a role in locomotion, as Adams and Tyler (1980) suggested, sediment type would be expected to have a greater effect than food input. As mentioned previously, there is a change in sediment composition from calcareous foraminiferal muds at 5°N to fine-grained clays at 9°N (Berelson *et al.*, 1995; Stephens *et al.*, 1997). This coincides with a shift from tail shape 2 (clavate-conicocylindrical) to tail shape 1 (rounded with blunt end) and would appear to confirm the importance of tail shape in locomotion.

Gerlach (1954) suggested that a blunt tail shape was characteristic of burrowing nematodes, as opposed to the interstitial dwellers of Wieser (1959). The fine-grained clays experienced at 9 and 23°N will most probably lack an interstitial system perhaps explaining the increased occurrence of tail shape 1 (rounded with blunt end) at these sites. However, as Wieser (1959) stated, the division of nematodes into interstitial and

burrowing forms *per se* is very difficult. So, in the absence of ecological underpinning for tail-shape groups 1-3, the reasons for this functional shift are unclear.

In a study of the functional group composition of some northern Atlantic nematodes, Thistle *et al.* (1995) suggested that using a two-way combined analysis of feeding groups and tail shapes provided additional ecological information not revealed by a single-classification analysis. They demonstrated that particular tail-shapes are not restricted to particular buccal morphologies and also that some combinations were present at some sites but absent from others. Thistle *et al.* (1995) proposed that combining the two classifications would better represent the true guild structure within nematode communities. In contrast to their study, the present work does not suggest that any additional, significant, ecological information is gained from using a two-way analysis. There are currently no good explanations why tail shape should be ecologically linked to feeding mechanisms. Until this information becomes available, a two-way analysis may only provide information on which groups are present or absent from a particular environment.

5.4 Conclusions

- Elevated POC flux is correlated with an increase in the abundance of 1A-(selective deposit feeders) type nematodes and a corresponding decrease in the abundance of 1B-type nematodes (non-selective deposit feeders). There was also a significant correlation between the abundance of 1A nematodes and microbial biomass. When combined with the results of other studies on trophic composition, this suggested that 1B may be the typical feeding strategy of deep-sea nematodes and 1As are found in areas of greater food availability.

- 2A nematodes (epistrate feeders) are found in areas receiving inputs of fresh phytodetritus. It is proposed that the greater number of 2A nematodes at 5°N represents a 'relict fauna' that reproduced during a possible recent phytodetrital event. 2A nematodes have been observed to feed on whole diatoms in shallow-water studies and the presence of intact diatoms in EqPac phytodetritus aggregates, and their presence in the guts of 2A nematodes suggests that the diet of 2A nematodes may be the same in the deep sea.

- Due to the presence of a correlation between a change in sediment type and tail shape representation, it is suggested that sediment type may have a much stronger structuring force on tail shape than food availability. This, in turn, suggests that tail shape may play an important role in nematode locomotion.

- There was no evidence observed to suggest that abundance of larger organisms influenced the vertical structure of nematode communities, as revealed by functional group composition. It was expected that rapid, vertical mixing of phytodetritus due to bioturbation by these organisms would cause changes in the proportion of feeding types such as 1A and 2A thought to utilise phytodetrital material or its associated microbial community. The absence of a significant change in the abundance of these two feeding types over the depth of influence by larger organisms suggests that bioturbation effects are not influencing the vertical structure of nematode communities.

6.1 Introduction

In addition to being the most abundant metazoans in deep-sea sediments, nematodes are also the most diverse. Lambshead (1993) estimated that there may be as many as 10^7 species of marine nematode in deep-sea sediments alone. Observations appear to support this hypothesis; in a sample of 216 nematodes, Hope (in Spiess *et al.*, 1987) recorded a surprising 148 species. Deep-sea nematode species diversity may also be approximately one order of magnitude greater than macrofaunal diversity. Certainly in the Rockall Trough, NE Atlantic, a study found polychaete diversity to be an order of magnitude lower than nematode diversity (Lambshead, 1993). Species evenness is also high - a feature very characteristic of the benthic fauna of the deep sea.

Five years before Connell (1978) proposed the Intermediate Disturbance Hypothesis, Grassle and Sanders (1973) observed that habitats are made up of a mosaic of patches, each at a different stage of recovery from a disturbance event. They argued that these patches were important for maintaining high species diversity over ecological timescales. Connell (1979) later demonstrated that maximum diversity could be attained if disturbance events occurred with intermediate frequency, severity or size of the area perturbed (see review in Chapter 2). For example, if a disturbance event kills all organisms over a very large area, then recolonisation in the centre of the patch comes only from those organisms capable of travelling great distances and able to become established in very exposed conditions. Alternatively, if the openings created by a disturbance event are small, the ability to colonise and grow in the presence of resident competitors is very important and again the colonisers will be only a subset of the total species pool. When disturbance creates intermediate-sized openings, both types of organisms may be equally competitive so both colonise and diversity is highest.

Disturbance has been defined as a discrete, punctuated killing or displacement that creates an opportunity for new individuals to become established (see chapter 2, section 2.1, also Sousa, 1984). The processes that create disturbance are very varied and are often habitat-specific. Those processes that are characteristic of the deep sea have been described in

detail in Chapter 2 and may be physical (e.g. benthic storms) or biotic (e.g. bioturbation effects). The deposition of phytodetritus, however, causes neither a punctuated killing or displacement and therefore is perhaps better thought of as an enrichment event. Soon after the discovery of rapid, vertical transport of phytoplankton aggregates to the deep-sea floor (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986), Gooday (1988) documented the first evidence of a meiofaunal response to this low-level enrichment. Foraminiferal assemblages were found to preferentially migrate into phytodetrital aggregates and subsequently undergo rapid reproduction. One of these foraminiferans was found only occasionally in sediments that had not received an input of phytodetritus (Gooday, 1990).

Whilst the phytodetrital material may sink and arrive at the seafloor as a uniform covering, subsequent resuspension and deposition around mounds and depressions on the seabed result in a patchy distribution of phytodetritus on a scale of centimetres to tens of centimetres, that persists for at least months (Rice and Lambshead, 1994). The patchy distribution of the holothurian, *Benthogone rosea* was thought to reflect this patchy distribution of the phytodetritus on which it feeds (Gooday and Turley, 1990).

Grassle and Morse-Porteous (1987) and Grassle (1989) emphasised an important role played by these organic patches in the maintenance of high diversity in deep-sea sediments, against a backdrop of low environmental productivity. Within a patch, a single species may be abundant, such as the foraminiferan described by Gooday (1990), and diversity may be reduced on a microhabitat scale. However, on a larger scale, higher regional diversity was postulated to be maintained by the combined input of these small patches that increase habitat heterogeneity and, therefore, the species pool (Grassle and Maciolek, 1992).

Knowledge of the effects of sub-catastrophic organic inputs on nematode communities are known only from shallow-water environments. In the Clyde estuary, Lambshead (1986) demonstrated, using neutral model analysis, that cores from sites receiving elevated organic inputs had a significantly higher diversity than cores from a reference site.

In the deep sea, Paterson *et al.* (1998) attempted to examine the effects of elevated surface productivity on abyssal polychaete communities, but could find no correlation between

species richness and overlying surface-water productivity. Lambshead (1993) suggested that increased nutrient flux to the deep-sea floor will, on average, lead to higher dominance and hence lower sample diversity. However, Smith *et al.*. (1998) hypothesised that release of organic materials from a whale skeleton in the San Diego Trough caused a sharp increase in sample diversity in macrofauna, by excluding the dominant species in the immediate vicinity of the skeleton.

Currently, the influence of phytodetritus and elevated POC flux on local and regional nematode species diversity has not been established. The present chapter will use detailed taxonomic analyses of EqPac nematode communities to test the following hypotheses:

- Elevated POC flux and/or phytodetritus standing crop are not correlated with nematode α (within-habitat) or β (between-habitat) diversity

- Elevated POC flux and/or phytodetritus standing crop are not correlated with changes in the species-level community structure of nematodes in the abyssal, equatorial Pacific

6.2 Results

Nematode species lists for the 0-1cm sediment layer at each site and vertically in the sediment at 0, 5 and 9°N are detailed in appendices A and B respectively.

6.2.1 Horizontal Patterns of Species Diversity

6.2.1.1 Dominant Families and Genera

Twenty-five families were recorded from the equatorial station and all were found at least at one other station. The maximum number of families (26) was recorded from 2°N because of a family unique to that station, the Tripyloididae. Subsequently, the number of families decreased with increasing latitude to a minimum of 21 families at 9 and 23°N. Dominant families (>10%) recorded along the transect were divided into two communities (Table 6.1). At stations from 0-5°N, the dominant families were the Monhysteridae, the Chromadoridae and the Microlaimidae. At stations from 9-23°N, the Monhysteridae and the Chromadoridae were also dominant families, but the Microlaimidae were replaced by the Xyalidae. The Oxystominidae were a subdominant family (>5%) at all stations and the Microlaimidae were subdominant at stations 9 and 23°N. At the 0-5°N stations, other subdominant families varied from station to station (Table 6.1).

At the genus level, *Thalassomonhystera* was the dominant genus at all stations, varying from 18% at the equatorial station to 33% at 9 and 23°N. *Acantholaimus* also occurred with a high frequency at all stations. Other dominant to subdominant genera (>5% and >1%) included *Halalaimus, Microlaimus, Molgolaimus, Leptolaimus* and *Aponema*. The patterns of dominant and subdominant genera varied from station to station, but followed the general replacement of the Microlaimidae by the Xyalidae between 5 and 9°N (Table 6.2).

The total number of species recorded at each station reached a maximum of 124 at the equator and then decreased with increasing latitude to 81, recorded at 23°N (see species richness curves). At the species level, there were a small number of species that showed a distinct pattern with changing latitude. The distributions of the 20 most dominant species were plotted against latitude (Figure 6.1). *Thalassomonhystera sp. A, T.sp.G* and

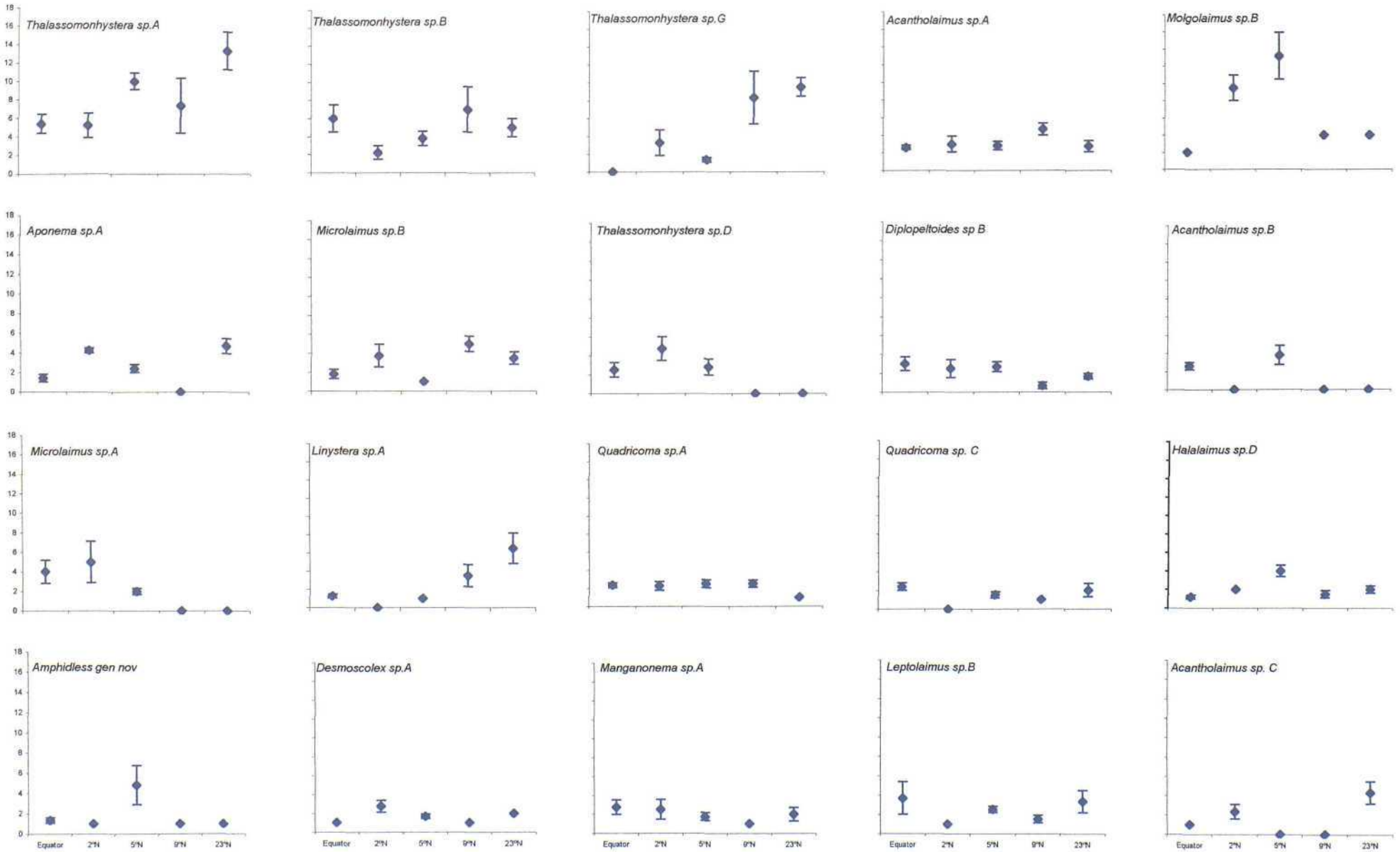
Table 6.1 Dominant (>10%) and subdominant (>5%) families present in 0-1cm sediment layer from 0-23°N
(the next most dominant family < 5% is also shown for convenience)

Equator		2°N		5°N		9°N		23°N	
MONHYSTERIDAE	32.13	MONHYSTERIDAE	28.20	MONHYSTERIDAE	29.53	MONHYSTERIDAE	36.05	MONHYSTERIDAE	32.92
CHROMADORIDAE	10.43	MICROLAIMIDAE	20.89	MICROLAIMIDAE	23.49	XYALIDAE	13.27	XYALIDAE	18.43
MICROLAIMIDAE	8.09	CHROMADORIDAE	9.66	CHROMADORIDAE	11.40	CHROMADORIDAE	9.18	CHROMADORIDAE	10.32
LEPTOLAIMIDAE	6.81	XYALIDAE	6.79	OXYSTOMINIDAE	5.35	OXYSTOMINIDAE	6.46	MICROLAIMIDAE	8.60
XYALIDAE	6.38	DESMOSCOLECIDAE	6.53	MEYLIIDAE	3.95	MICROLAIMIDAE	6.46	OXYSTOMINIDAE	5.65
AEGIALOALAIMIDA	5.74	OXYSTOMINIDAE	3.92			AEGIALOALAIMIDA	4.42	LEPTOLAIMIDAE	4.67
MEYLIIDAE	5.32								
DIPLOPELTIDIDAE	4.89								

Table 6.2 Dominant (> 5%) and subdominant (> 1%) genera for 0-1cm sediment layer for stations 0-23°N
(the next most dominant genus < 1% is also shown for convenience at each station)

Equator			2°N		5°N		9°N		23°N
Thalassomonhystera	18.27	*Thalassomonhystera*	22.88	*Thalassomonhystera*	22.78	*Thalassomonhystera*	32.47	*Thalassomonhystera*	32.08
Acantholaimus	9.63	*Microlaimus*	7.06	*Molgolaimus*	8.46	*Acantholaimus*	5.90	*Acantholaimus*	7.27
Quadricoma	5.68	*Molgolaimus*	6.78	*Acantholaimus*	7.59	*Halalaimus*	5.54	*Linhystera*	6.52
Leptolaimus	5.43	*Acantholaimus*	5.65	*Microlaimus*	5.42	*Microlaimus*	4.06	*Halalaimus*	5.26
Microlaimus	5.19	*Desmoscolex*	5.08	*Amphidless gen nov*	5.21	*Leptolaimus*	4.06	*Theristus*	4.01
Diplopeltiodes	5.19	*Aponema*	4.80	*Aponema*	4.56	*Desmoscolecidae*	2.58	*Aponema*	3.51
Halalaimus	3.46	*Diplopeltiodes*	3.11	*Halalaimus*	3.69	*Linhystera*	2.58	*Microlaimus*	3.51
Desmodora	3.21	*Halalaimus*	2.82	*Quadricoma*	2.82	*Manganonema*	2.58	*Leptolaimus*	3.51
Diplopeltula	2.96	*Quadricoma*	2.54	*Desmodora*	2.60	*Diplopeltula*	2.58	*Aegialoalaimus*	2.51
Manganonema	2.72	*Ascolaimus?*	2.26	*Leptolaimus*	2.39	*Aegialoalaimus*	2.21	*Daptonema*	2.26
Thalassomonhystera	2.47	*Syringolaimus*	1.98	*Diplopeltiodes*	2.39	*Quadricoma*	2.21	*Manganonema*	2.01
Monhysteridae?	2.47	*Nox*	1.98	*Ascolaimus*	2.17	*Prochromadorella*	1.85	*Diplopeltiodes*	1.75
Desmoscolex	2.22	*Campylaimus*	1.98	*Manganonema*	1.95	*Desmodora*	1.85	*Desmoscolex*	1.75
Actinonema	1.98	*Desmoscolecidae*	1.69	*Syringolaimus*	1.74	*Diplopeltiodes*	1.85	*Neochromadora?*	1.25
Camacolaimus	1.73	*Monhysteridae?*	1.69	*Tubolaimoides*	1.74	*Cobbia*	1.85	*Pselionema*	1.25
Aponema	1.73	*Actinonema*	1.41	*Cervonema*	1.30	*Syringolaimus? indet j*	1.48	*Quadricoma*	1.25
Linhystera	1.23	*Desmodora*	1.41	*Xyalidae?*	1.30	*Molgolaimus*	1.48	*Campylaimus*	1.25
Molgolaimus	0.99	*Linhystera?*	1.41	*Acantholaimus?*	1.08	*Nox*	1.11	*Actinonema*	1.00
Eudraconema	0.99	*Manganonema*	1.41	*Desmoscolex*	1.08	*Desmoscolex*	1.11	*Desmodora*	1.00
Campylaimus	0.99	*Phanodermatidae*	1.13	*Linhystera*	1.08	*Amphimonhystera*	1.11	*Molgolaimus*	1.00
Amphidless gen nov	0.99	*Rhips?*	1.13	*Oxystomina*	0.87	*Linhomoeidae?*	1.11	*Metadesmolaimus*	1.00
Tubolaimoides	0.74	*Eudraconema*	1.13			*Litinium*	0.74	*Southerniella*	1.00
Tricoma/Quadricoma?	0.74	*Microlaimidae*	1.13					*Bathyeurystomina*	0.75
Syringolaimus	0.74	*Pselionema*	1.13						
Pselionema	0.74	*Prochromodorella?*	0.85						

Figure 6.1 (shown overleaf) Species distributions for the 20 most dominant nematode species in the 0-1cm sediment layer at five stations from 0-23°N in the abyssal Pacific. The mean abundance of each species (as % of total individuals per sample) at each station is shown on the y-axis. Error bars are ± 1s.e.


Thalassomonhystera sp.A
Thalassomonhystera sp.B
Thalassomonhystera sp.G
Acantholaimus sp.A
Molgolaimus sp.B
Aponema sp.A
Microlaimus sp.B
Thalassomonhystera sp.D
Diplopeltoides sp B
Acantholaimus sp.B
Microlaimus sp.A
Linystera sp.A
Quadricoma sp.A
Quadricoma sp. C
Halalaimus sp.D
Amphidless gen nov
Desmoscolex sp.A
Manganonema sp.A
Leptolaimus sp.B
Acantholaimus sp. C
Equator
2°N
5°N
9°N
23°N

Lynhystera sp.A all increased markedly in abundance with increasing latitude and *Microlaimus sp.A* showed a corresponding decrease with increasing latitude. There were few linear patterns amongst the remaining dominant (>2%) species (Figure 6.1). A drop in numbers of *T. sp. B* correlated well to an increase in the numbers of *T. sp. D* at 2°N, and numbers of the microlaimid *Aponema sp. A* were highest at 23°N. This corresponded to a decrease in the other microlaimids found, namely *Molgolaimus, sp. B, Microlaimus sp. A* and *Microlaimus sp. B*. Although an important family, the xyalids were not represented by any particularly abundant species and consequently were not seen in the dominant species lists. Species belonging to the genus *Acantholaimus* were represented by small numbers of individuals per species.

6.2.1.2 α (Within-habitat) Diversity

When the samples were combined into two groups, 0-5°N (stations that do receive phytodetritus) and 9-23°N (stations that do not receive phytodetritus), all indices of α diversity were significantly different ($P < 0.05$) with the exception of Margalef's D ($P = 0.0796$ using a Mann-Whitney U-test). Whilst it is mathematically incorrect to combine sample values rather than mean values per station for statistical analysis, due to problems with pseudoreplication, this has been discussed in chapter 3 (section 3.1.2) and was considered acceptable in this study.

Along the transect, Shannon diversity index (H', using log base 2) values indicated a decrease with increasing latitude in the top 0-1cm sediment layer (Figure 6.2) although this was not significant (Table 6.3). Values of H' at 23°N were significantly different from each H' value at the equator, 2 and 5°N ($P \leq 0.03$, using a Mann-Whitney U-test). The mean H' value at 9°N was not significantly different from any other station ($P > 0.371$, using a Mann-Whitney U-test) although this is possibly due to the high variation in intra-station abundance (see chapter 4, section 4.3) and small number of samples (3) from this site (type I error).

Pielou's evenness index, J' followed a similar pattern to H' which was expected due to the strong inter-relationship between the two indices. J' decreased with increasing latitude in the top (0-1cm) sediment layer (Figure 6.2), but this change was not significant (Table 6.3). There was no significant decrease in Margalef's index of species richness, D, ($P =$

Figure 6.2 Mean α diversity values for 0-1cm sediment layer at all EqPac stations. Error bars are ± 1s.e.

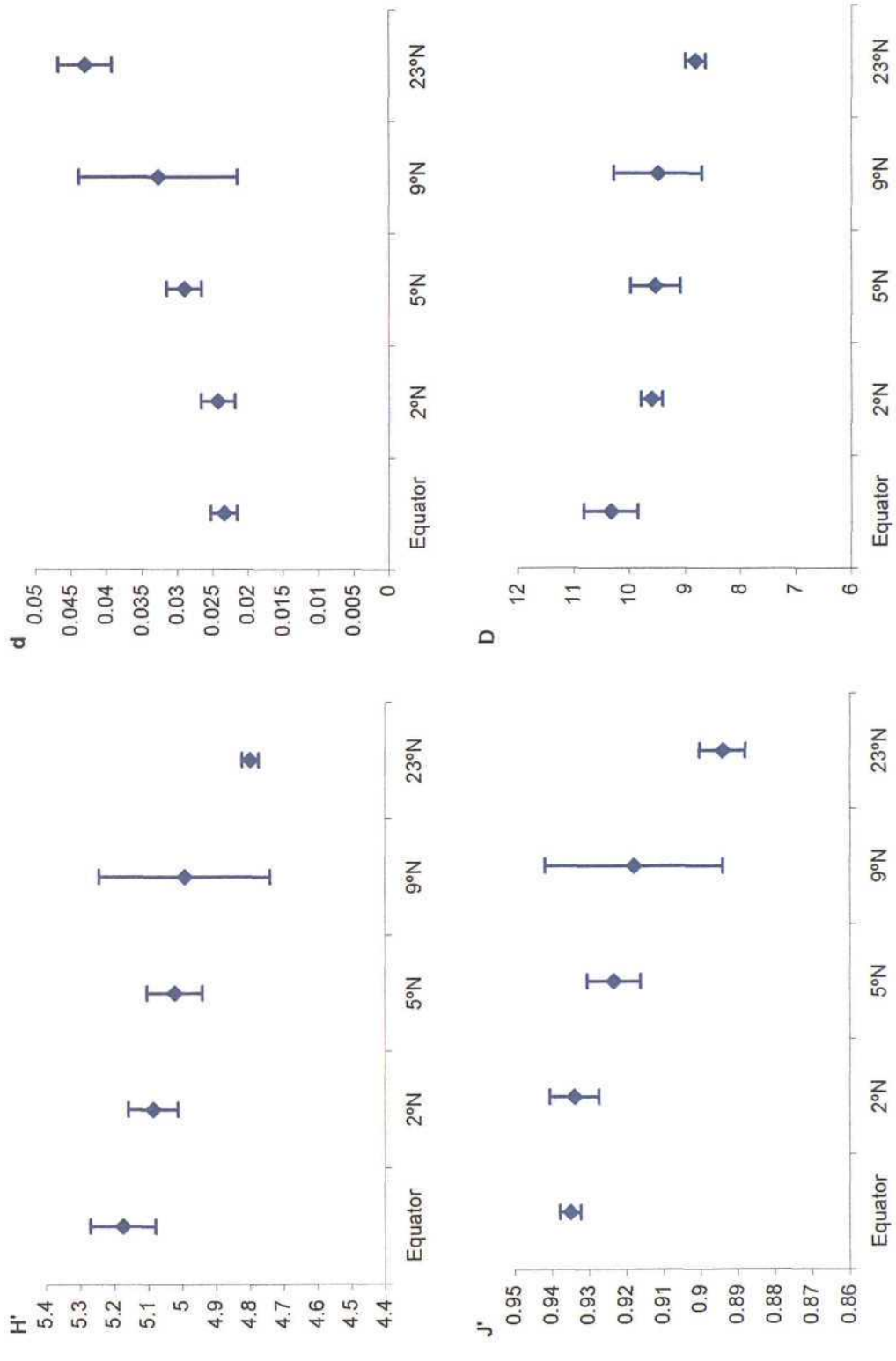


Table 6.3 Values of H', J', Margalef's D and Simpson's d for 0-1cm sediment layer at stations 0-23°N, including Kruskal-Wallis test statistic, Z.

H'	Equator	2°N	5°N	9°N	23°N	
	4.898	5.049	4.771	5.231	4.774	
	5.371	4.899	4.973	4.489	4.754	
	4.998	5.232	5.233	5.257	4.8	
	5.337	5.161	5.161		4.865	
	5.265		4.972			
Mean	5.174	5.085	5.022	4.992	4.798	
1s.e.	0.095	0.073	0.081	0.252	0.024	
Z	1.900	0.630	0.170	-0.200	-2.690	$P = 0.062$

J'	Equator	2°N	5°N	9°N	23°N	
	0.938	0.927	0.904	0.934	0.902	
	0.944	0.920	0.937	0.871	0.876	
	0.929	0.950	0.926	0.949	0.902	
	0.929	0.939	0.940		0.897	
	0.935		0.910			
Mean	0.935	0.934	0.923	0.918	0.894	
1s.e.	0.003	0.007	0.007	0.024	0.006	
Z	1.4	1.07	0	0.1	-2.69	$P = 0.081$

D	Equator	2°N	5°N	9°N	23°N	
	9.207	9.533	8.625	10.565	8.564	
	11.150	9.102	8.667	7.942	9.101	
	9.089	10.025	11.084	9.930	8.432	
	11.196	9.731	9.640		9.101	
	11.029		9.640			
Mean	10.334	9.598	9.531	9.479	8.799	
1s.e.	0.485	0.194	0.447	0.790	0.176	
Z	1.65	0.54	-0.17	0	-2.15	$P = 0.193$

d	Equator	2°N	5°N	9°N	23°N	
	0.027	0.026	0.037	0.023	0.037	
	0.018	0.030	0.027	0.055	0.054	
	0.028	0.019	0.026	0.020	0.040	
	0.023	0.022	0.023		0.041	
	0.021		0.032			
Mean	0.023	0.024	0.029	0.033	0.043	
1s.e.	0.002	0.002	0.002	0.011	0.004	
Z	-1.53	-1.21	0.37	-0.2	2.64	$P = 0.068$

0.193) with increasing latitude (Figure 6.2, Table 6.3). Simpson's d, a diversity index that provides some measure of species dominance, did not indicate a significant increase (Table 6.3) with increasing latitude (Figure 6.2).

Composite rarefaction curves were plotted for each station by calculating the mean expected number of species at each knot. This procedure has been used previously by other authors (Boucher and Lambshead, 1995) and was considered acceptable in the present study. The composite curves display the drop in diversity and evenness with increasing latitude that was noted above. Figure 6.3 indicates how, with the exception of samples from stations at 2° and 5°N, the rarefaction curves become progressively less steep with increasing latitude. At 2° and 5°N the rarefaction curves overlap for much of the curve.

A Kruskal-Wallis test indicated no significant difference ($P = 0.463$) in Caswell's V-statistic (Table 6.4) and there was no clear pattern of increasing dominance with increasing latitude in the 0-1cm sediment layer as indicated by the mean V-statistic for each station (Table 6.4).

The *k*-dominance curves for each station were very similar and so the data from all replicates were pooled and a mean value for each species rank was plotted (Figure 6.4). This approach has been used before as a method for comparing stations (Austen and Warwick, 1989). The equatorial station has the most even species distribution and then the nematode communties show increasing dominance with increasing latitude. Between the equator and 9°N, the curves for 0-2°N and 5-9°N cross, so their diversity should not be compared directly.

6.2.1.3 β (Between-habitat) Diversity

The total number of species recorded along the transect as a whole was 225 species compared with 81-124 that was the range recorded per individual station. The β diversity measure of species richness showed a separation of the curves with latitude (Figure 6.5). The collector's curve for the equatorial station was highest and minimum values occurred at 23°N. Also, except for the curve for 23°N, none showed signs of levelling, indicating that the expected maximum number of species in the community at these stations had not

Figure 6.3 Mean rarefaction curves for 0-1cm sediment layer at all EqPac stations.

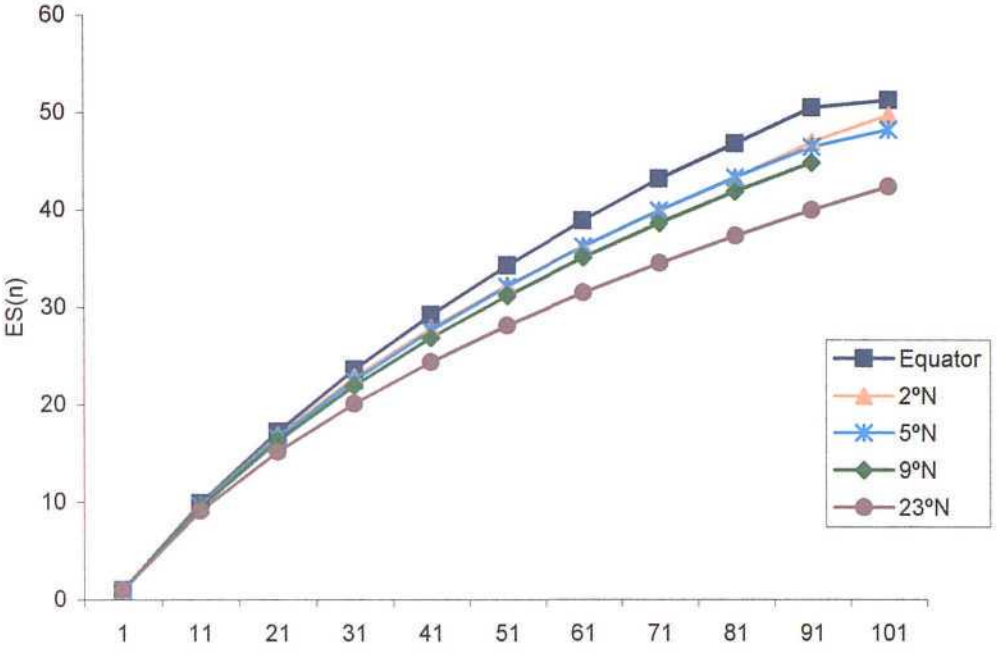


Table 6.4 Neutral model V-values for 0-1cm sediment layer with Kruskal-wallis test statistic, Z

	Equator	2°N	5°N	9°N	23°N
	-1.723	-0.375	-1.329	-0.495	-1.039
	-0.499	-0.882	0.732	-1.987	-2.354
	0.407	0.994	-2.120	0.876	-0.333
	-1.691	0.413	0.441		-1.309
	-1.522		-1.611		
Mean	-1.006	0.038	-0.777	-0.535	-1.259
1s.e.	0.419	0.415	0.573	0.827	0.419
Z	-0.91	1.7	-0.17	0.3	-0.81

$P = 0.463$

Figure 6.4 Mean *k*-dominance curves for 0-1cm sediment layer at all EqPac stations.

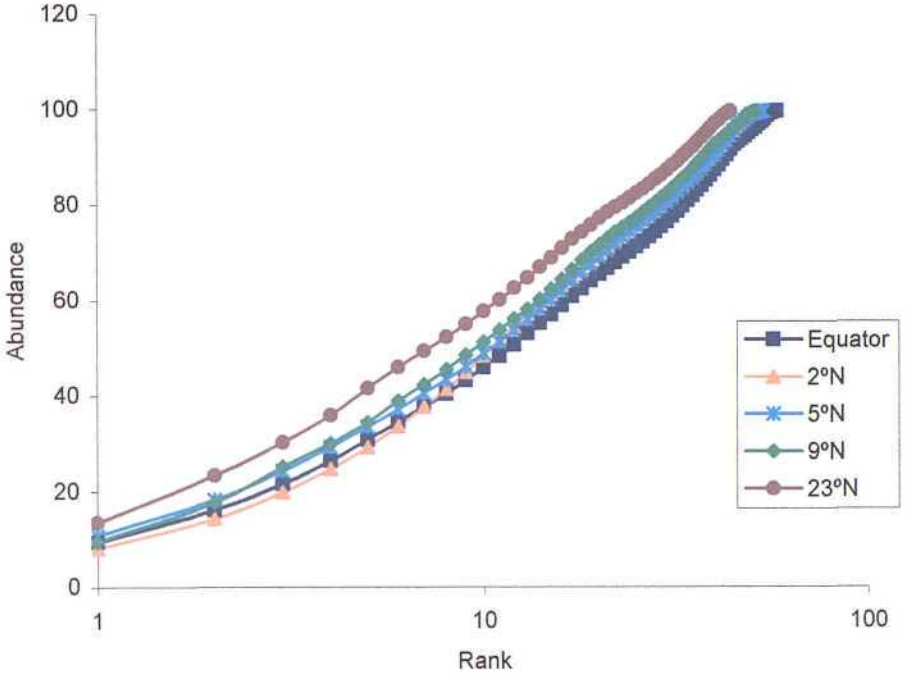
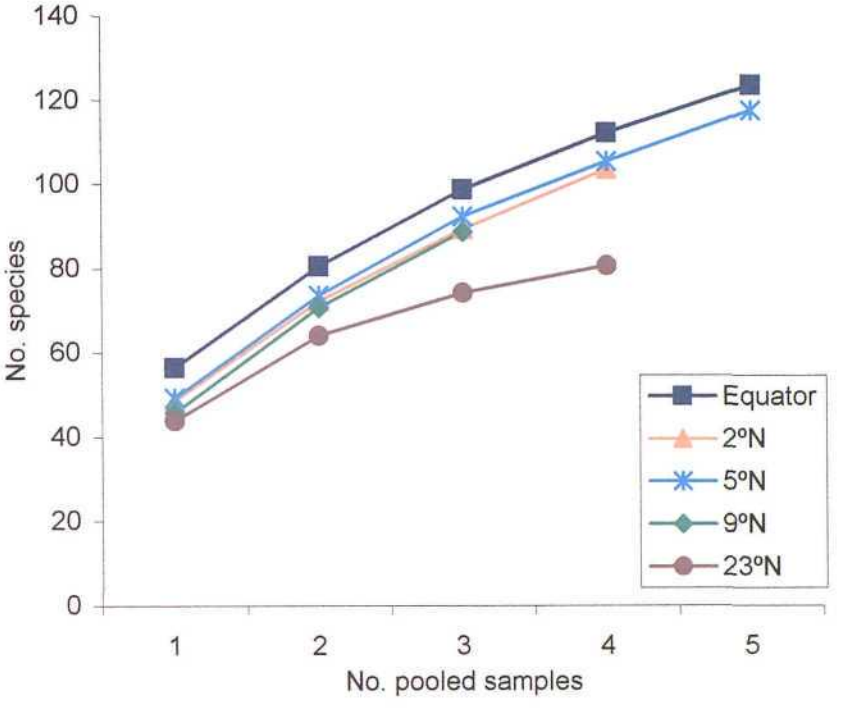


Figure 6.5 Species richness curves for 0-1cm sediment layer at all EqPac stations.



been observed. This might have been achieved either by identifying a greater number of individuals from each sample or using a greater number of replicates, had time permitted.

6.2.1.4 Multivariate Analyses

The stations were grouped *a priori* (before any statistical analysis to avoid bias) into two groups containing stations 0-5°N and 9-23°N, and tested using a pairwise, crossed ANOSIM for both untransformed and double-root (√√) -transformed data. The two groups were significantly different for both data sets ($P = 0.002$). The results of a pairwise, crossed ANOSIM analysis for samples grouped per station, also both untransformed and √√-transformed, are given in table 6.5. All stations were significantly different from each other, even when the data had been severely transformed.

Cluster analysis, using the Bray-Curtis index of similarity (single link), demonstrated this grouping. At a similarity of 37.5%, the samples were divided into the same two groups defined *a priori* to ANOSIM analysis (Figure 6.6a). At 40% similarity, the samples from 2°N separated from 0 and 5°N. It is interesting to note that nematode community structure at the equator was more similar to that at 5°N than either was with the community at 2°N.

After √√-transformation there was a division into two groups at 40% similarity. At 50% similarity, the groups were divided into their respective stations (Figure 6.6b). A number of exceptions did occur; sample BC19 from 9°N was still found in the 23°N cluster, even after transformation this grouping occurred at 50% similarity, and sample BC4 from the equatorial station was found on its own. As the data entry order can influence the final cluster arrangement, the sample data was re-entered in random order and the cluster analysis repeated (Figure 6.7). The overall clustering was not greatly changed, although the position of sample BC4 from the equatorial station moved as the dissimilarity between it and the other equatorial samples increased.

NMDS ordination of the data is shown in figure 6.8 for both untransformed and √√-transformed data. The stations formed discrete clusters, with the exception of 9 and 23°N which were grouped together. The stress value was high for both ordinations and consequently, the groups formed in the cluster analysis at the 37% and 40% similarities (untransformed) and 40% and 50% (√√-transformed) were superimposed upon the NMDS

Table 6.5 ANOSIM results for comparison of species data. (a) summary of all pairwise comparisons for stations at 0-23°N untransformed data and (b) root-root transformed data

(a)

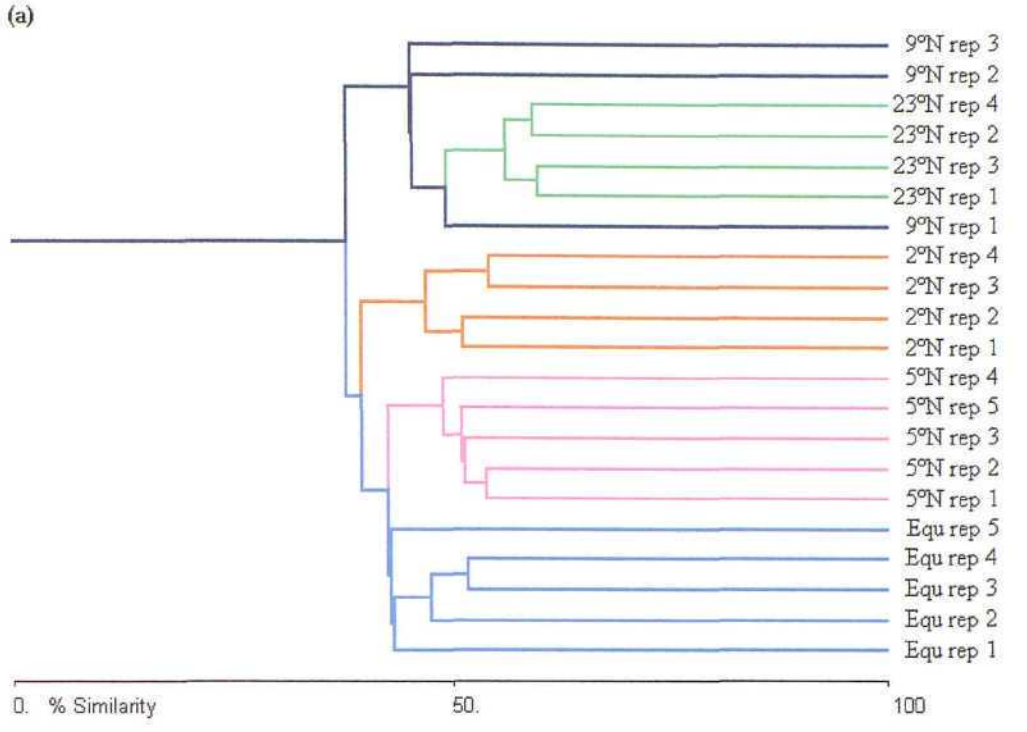
2°N	*			
5°N	*	*		
9°N	+	+	+	
23°N	*	+	*	+
	Equator	2°N	5°N	9°N

(b)

2°N	*			
5°N	*	*		
9°N	+	+	+	
23°N	*	+	*	+
	Equator	2°N	5°N	9°N

p > 5% + p > 1% *

Figure 6.6 Cluster analysis for species data for 0-1cm sediment layer at all EqPac stations based upon the Bray-Curtis similarity index (single link). (a) untransformed data and (b) double-root (√√) -transformed data.



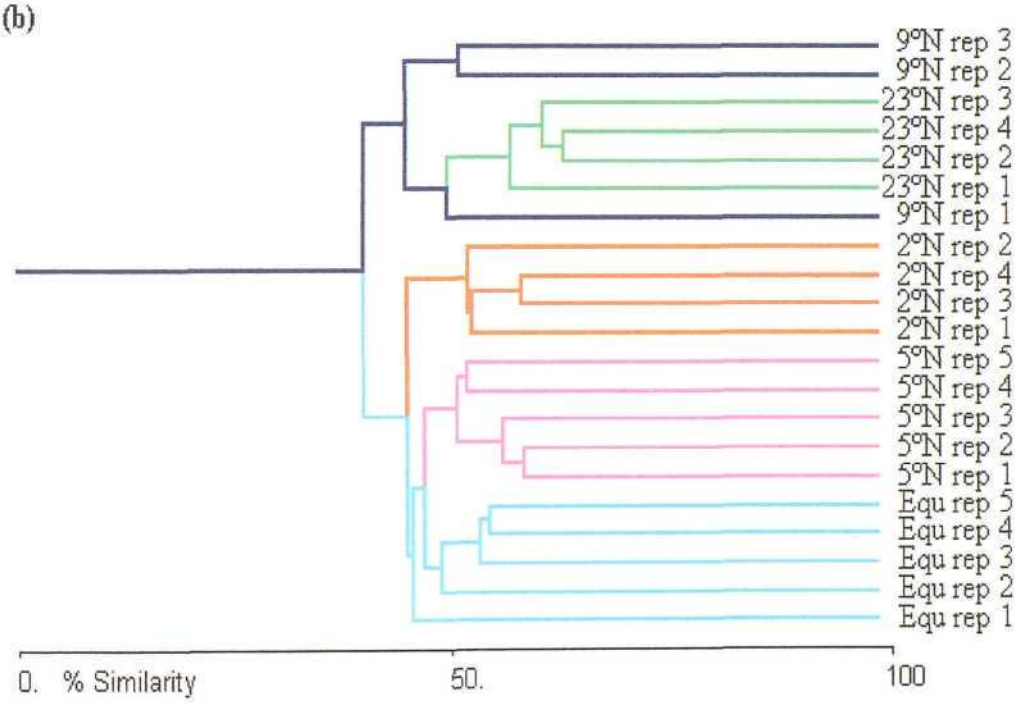


Figure 6.7 Cluster analysis for species data for 0-1cm sediment layer at all EqPac stations based upon the Bray-Curtis similarity index (single link). Sample data was entered randomly (i.e. not in station order).

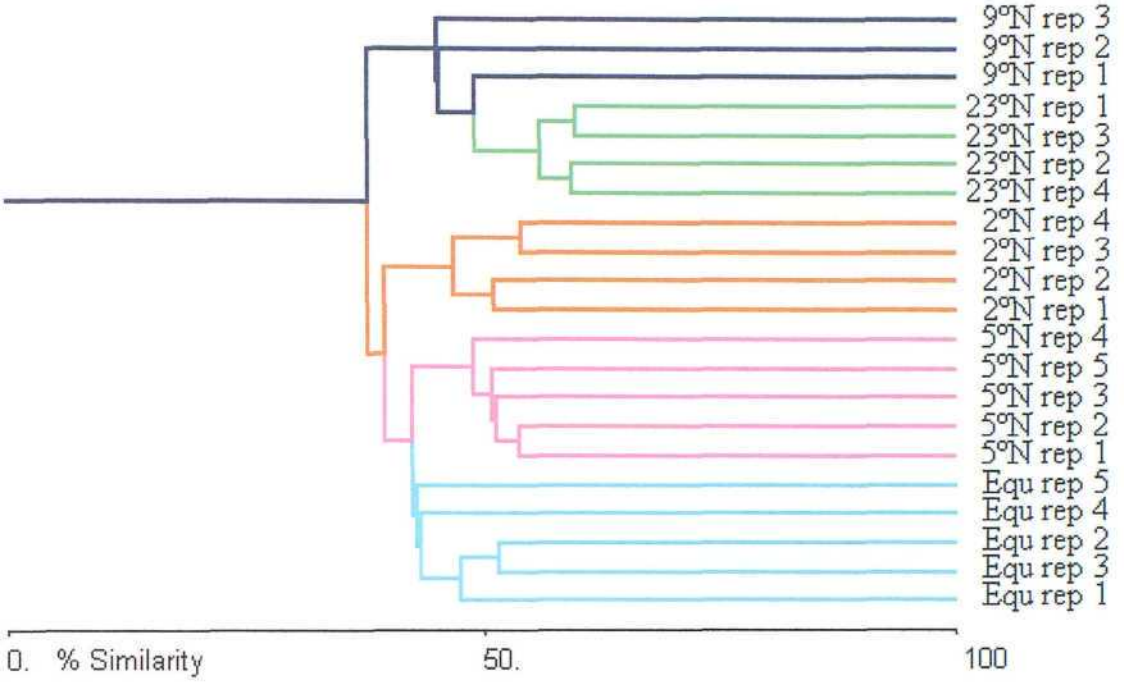
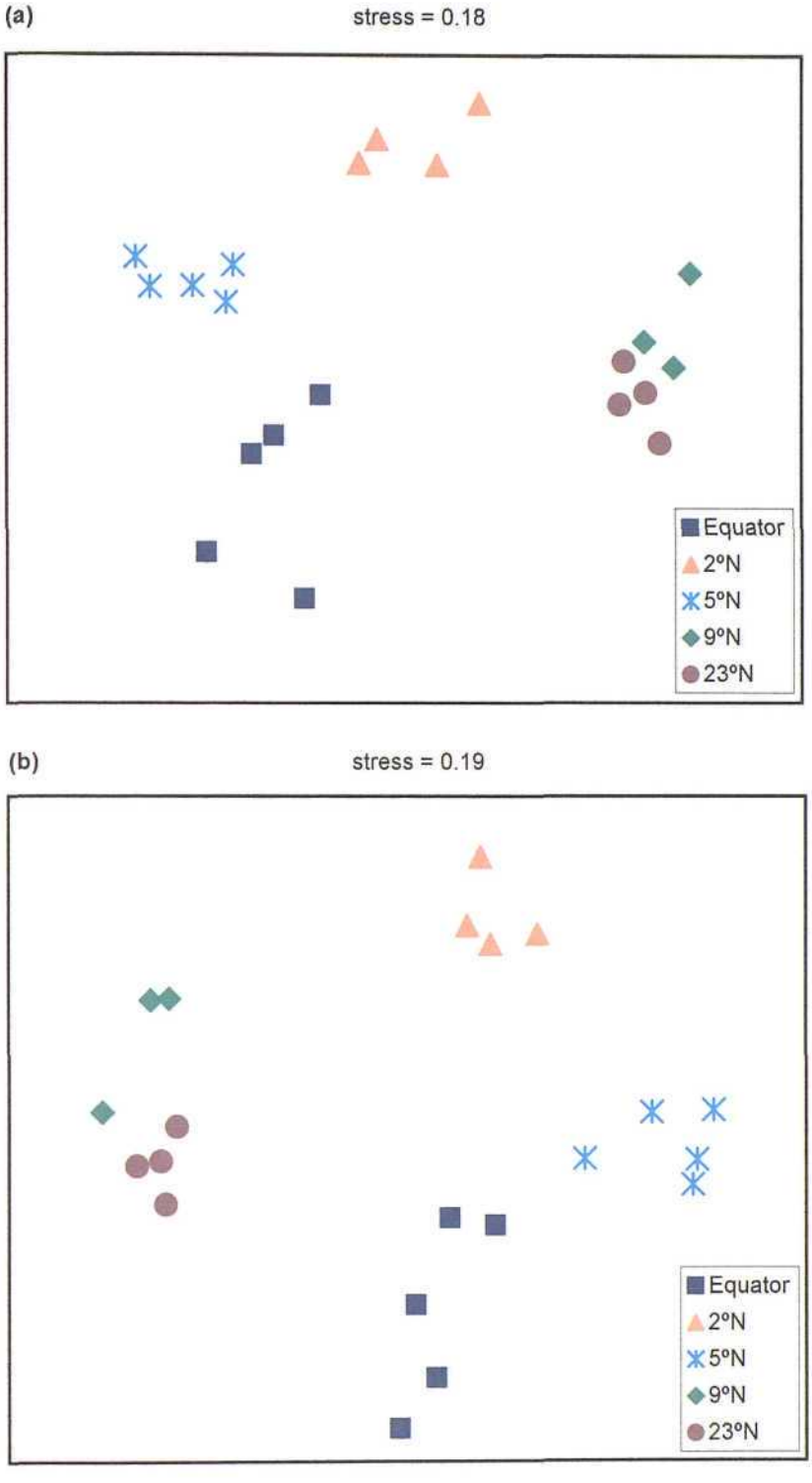


Figure 6.8 NMDS results for data for 0-1cm sediment layer at all EqPac stations based upon comparisons of species lists. (a) untransformed data and (b) √√-transformed data



plots (Figure 6.9). The cluster analysis groupings reinforce the NMDS clusters rather than distorting the ordinations.

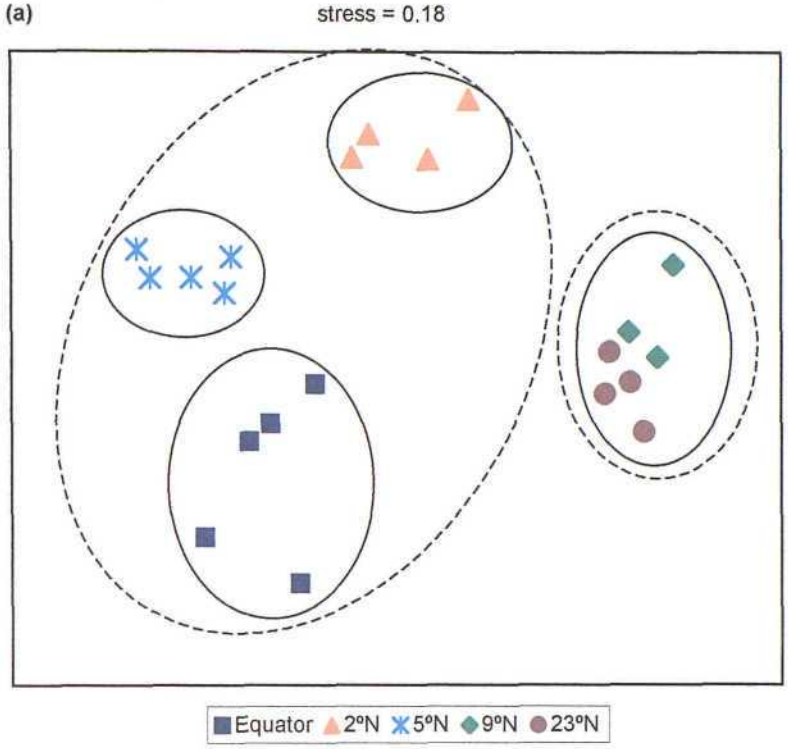
6.2.2 Vertical Patterns of Species Distribution

6.2.2.1 Dominant Families, Genera and Species

At the equatorial station, the number of families dropped from 23 in the surface layer to 17 below the 2cm sediment horizon. The number of families represented in the surface layer is fewer than in the previous section, due to the smaller number of replicates used in the analysis. At 9°N, there was no decrease in the total number of families until the 3cm sediment horizon, where the number of families dropped from 21 to 19. At all three stations, the dominant families (>10%) below the 2cm horizon were the Monhysteridae, Ironidae and Xyalidae, although at 9°N these families were also dominant in the 1-2cm layer (Table 6.6). In the 0-2cm sediments at the equatorial station and at 5°N, the Monhysteridae were still the most common, but the Ironidae and Xyalidae were replaced by the Chromadoridae and Microlaimidae respectively (Table 6.6). Subdominant families (> 5%) at all sediment depths at the equatorial station included the Leptolaimidae, but the Oxystominidae, Meyliidae and Aegialoalaimidae were also present in abundances greater than 5% in the surface (0-1cm) sediment layer (Table 6.6). At 5°N, the Chromadoridae were subdominant at all sediment depths and the Desmoscolecidae, Meyliidae and Oxystominidae were subdominant in the 0-1cm layer. At 9°N the Chromadoridae and also the Oxystominidae were subdominant at all depths in the sediment (Table 6.6).

Dominant and subdominant genera are listed in Table 6.7. At the genus level there was marked dominance by two genera (*Thalassomonhystera* and *Syringolaimus*) at all depths below the 2cm horizon, that accounted for approximately half of all the individuals identified. Above the 2cm horizon, this dominance was less marked in the samples from the equator and 5°N. *Syringolaimus* was not present as a subdominant genus and was replaced by a number of others including *Acantholaimus, Cobbia* and *Molgolaimus*. At 9°N, *Syringolaimus* was the dominant genus in the 1-2cm sediment layer, although it had also almost disappeared in the surface layer, to be replaced by *Acantholaimus* and *Halalaimus*.

Figure 6.9 NMDS results for data for 0-1cm sediment layer at all EqPac stations based upon comparisons of species data with cluster-analysis groups superimposed. (a) untransformed data, where the solid line represents 37% and the dashed line 40% similarity, and (b) √√-transformed data, where the solid line represents 40% and the dashed line 50% similarity.



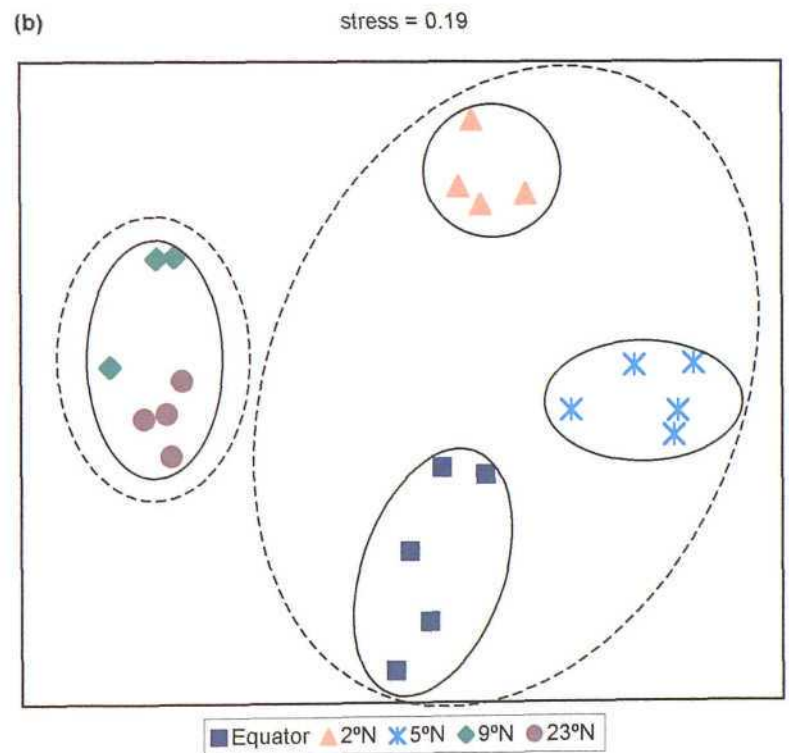


Table 6.6 Dominant (>10%) and subdominant (>5%) families present in 0-5cm sediment layers from 0, 5 and 9°N

Equator

0-1cm	Mean no.	%	1-2cm	Mean no.	%	2-3cm	Mean no.	%	3-5cm	Mean no.	%
MONHYSTERIDAE	30.000	33.09	XYALIDAE	28.667	28.38	MONHYSTERIDAE	28.667	31.16	IRONIDAE	27.667	28.23
CHROMADORIDAE	10.333	11.40	MONHYSTERIDAE	26.667	26.40	XYALIDAE	13.333	14.49	MONHYSTERIDAE	17.000	17.35
XYALIDAE	6.000	6.62	CHROMADORIDAE	7.667	7.59	IRONIDAE	9.667	10.51	DESMOSCOLECIDAE	13.333	13.61
MEYLIIDAE	5.667	6.25	LEPTOLAIMIDAE	6.667	6.60	LEPTOLAIMIDAE	7.333	7.97	XYALIDAE	9.667	9.86
LEPTOLAIMIDAE	5.000	5.51	OXYSTOMINIDAE	5.000	4.95	OXYSTOMINIDAE	5.333	5.80	LEPTOLAIMIDAE	5.667	5.78
AEGIALOALAIMIDA	4.667	5.15	MEYLIIDAE	5.000	4.95	CHROMADORIDAE	4.667	5.07	CHROMADORIDAE	4.667	4.76

5°N

0-1cm	Mean no.	%	1-2cm	Mean no.	%	2-3cm	Mean no.	%	3-5cm	Mean no.	%
MONHYSTERIDAE	25.333	28.04	MONHYSTERIDAE	33.333	36.90	MONHYSTERIDAE	38.667	36.94	IRONIDAE	33.000	41.08
MICROLAIMIDAE	17.667	19.56	XYALIDAE	17.667	19.56	IRONIDAE	23.667	22.61	MONHYSTERIDAE	16.667	20.75
DESMOSCOLECIDAE	8.000	8.86	CHROMADORIDAE	14.333	15.87	XYALIDAE	7.000	6.69	CHROMADORIDAE	6.333	7.88
CHROMADORIDAE	7.000	7.75	AEGIALOALAIMIDA	3.667	4.06	CHROMADORIDAE	6.667	6.37	XYALIDAE	5.000	6.22
XYALIDAE	6.667	7.38	OXYSTOMINIDAE	3.333	3.69	LEPTOLAIMIDAE	6.000	5.73	AXONOLAIMIDAE	4.000	4.98
OXYSTOMINIDAE	5.000	5.54	MICROLAIMIDAE	3.333	3.69	OXYSTOMINIDAE	4.000	3.82	LEPTOLAIMIDAE	3.667	4.56

9°N

0-1cm	Mean no.	%	1-2cm	Mean no.	%	2-3cm	Mean no.	%	3-5cm	Mean no.	%
MONHYSTERIDAE	35.000	36.08	IRONIDAE	22.000	27.50	MONHYSTERIDAE	33.000	31.63	IRONIDAE	39.667	40.48
XYALIDAE	12.333	12.71	MONHYSTERIDAE	20.000	25.00	IRONIDAE	24.667	23.64	MONHYSTERIDAE	22.667	23.13
CHROMADORIDAE	8.667	8.93	XYALIDAE	10.667	13.33	XYALIDAE	12.000	11.50	XYALIDAE	10.000	10.20
OXYSTOMINIDAE	6.333	6.53	CHROMADORIDAE	7.000	8.75	DIPLOPELTIDIDAE	9.000	8.63	CHROMADORIDAE	5.333	5.44
MICROLAIMIDAE	6.333	6.53	OXYSTOMINIDAE	5.333	6.67	CHROMADORIDAE	5.667	5.43	OXYSTOMINIDAE	3.333	3.40
AEGIALOALAIMIDA	4.667	4.81	DESMOSCOLECIDAE	3.667	4.58	OXYSTOMINIDAE	3.667	3.51	CYATHOLAIMIDAE	3.000	3.06

Table 6.7 Dominant (> 5%) and subdominant (> 1%) genera for 0-5cm sediment layers for stations 0, 5 and 9°N

Equator

0-1cm		%	1-2cm		%	2-3cm		%	3-5cm		%
Thalassomonhystera	16.67	18.73	*Thalassomonhystera*	26.67	26.49	*Thalassomonhystera*	28.67	31.05	*Syringolaimus*	27.67	28.23
Monhysteridae	11.67	13.11	*Cobbia*	22.67	22.52	*Syringolaimus*	9.67	10.47	*Thalassomonhystera*	17.00	17.35
Acantholaimus	7.67	8.61	*Acantholaimus*	6.33	6.29	*Cobbia*	8.67	9.39	*Desmoscolex*	12.33	12.59
Quadricoma	5.00	5.62	*Quadricoma*	5.00	4.97	*Quadricoma*	4.00	4.33	*Cobbia*	6.67	6.80
Diplopeltiodes	4.00	4.49	*Diplopeltiodes*	4.00	3.97	*Acantholaimus*	3.33	3.61	*Acantholaimus*	4.33	4.42
Desmodora	3.33	3.75	*Halalaimus*	3.33	3.31	*Camacolaimus*	3.33	3.61	*Camacolaimus*	4.33	4.42
Leptolaimus	3.33	3.75	*Leptolaimus*	3.33	3.31	*Ascolaimus*	3.33	3.61	*Quadricoma*	3.67	3.74
Halalaimus	3.00	3.37	*Camacolaimus*	2.33	2.32	*Litinium*	2.67	2.89	*Diplopeltiodes*	2.33	2.38
Actinonema	2.33	2.62	*Desmoscolex*	2.33	2.32	*Strange Chromadori*	2.67	2.89	*Litinium*	2.00	2.04
Desmoscolex	2.33	2.62	*Manganonema*	2.33	2.32	*Halalaimus*	2.33	2.53	*Linhystera*	1.67	1.70
Microlaimus	2.00	2.25	*Syringolaimus*	2.00	1.99	*Cyatholaimus*	2.33	2.53	*Leptolaimus*	1.33	1.36
Monhysteridae?	2.00	2.25	*Cyatholaimus*	2.00	1.99	*Manganonema*	2.33	2.53	*Manganonema*	1.33	1.36
Manganonema	2.00	2.25	*Molgolaimus*	2.00	1.99	*Desmoscolex*	2.00	2.17	*Molgolaimus*	1.00	1.02
Xyalidae	1.67	1.87	*Litinium*	1.67	1.66	*Leptolaimus*	1.67	1.81	*Greefiella*	1.00	1.02
Diplopeltula	1.67	1.87	*Xyalidae?*	1.67	1.66	*Diplopeltiodes*	1.67	1.81	*Amphidless gen nov*	1.00	1.02
Cervonema?	1.00	1.12	*Aponema*	1.00	0.99	*Linhystera*	1.67	1.81	*Diplopeltula*	1.00	1.02
Aponema	1.00	1.12	*Strange Chromadori*	1.00	0.99	*Araeolaimus?*	1.33	1.44			
			Linhystera	1.00	0.99	*Molgolaimus*	1.00	1.08			
			Ascolaimus	1.00	0.99	*Amphidless gen nov*	1.00	1.08			

Table 6.7 cont'd

5°N

0-1cm		%	1-2cm		%	2-3cm		%	3-5cm		%
Thalassomonhystera	21.00	21.14	*Thalassomonhystera*	33.33	33.56	*Thalassomonhystera*	38.67	36.94	*Syringolaimus*	33.00	41.08
Molgolaimus	7.33	7.38	*Acantholaimus*	12.33	12.42	*Syringolaimus*	22.67	21.66	*Thalassomonhystera*	17.33	21.58
Microlaimus	6.00	6.04	*Cobbia*	11.33	11.41	*Acantholaimus*	5.67	5.41	*Acantholaimus*	6.00	7.47
Amphidless gen nov	6.00	6.04	*Manganonema*	3.00	3.02	*Cobbia*	3.00	2.87	*Ascolaimus*	3.67	4.56
Acantholaimus	5.33	5.37	*Ascolaimus*	3.00	3.02	*Ascolaimus*	3.00	2.87	*Leptolaimus*	2.00	2.49
Monhysteridae	4.00	4.03	*Cervonema*	2.67	2.68	*Cyatholaimus*	2.67	2.55	*Cobbia*	2.00	2.49
Halalaimus	3.33	3.36	*Aponema*	2.67	2.68	*Leptolaimus*	2.67	2.55	*Linhystera*	2.00	2.49
Desmodora	3.33	3.36	*Leptolaimus*	2.33	2.35	*Amphimonhystera*	2.00	1.91	*Aegialoalaimus*	1.67	2.07
Aponema	3.33	3.36	*Amphidless gen nov*	2.33	2.35	*Camacolaimus*	1.67	1.59	*Pomponema?*	1.33	1.66
Quadricoma	3.33	3.36	*Halalaimus*	2.00	2.01	*Strange chromadori*	1.67	1.59	*Camacolaimus*	1.33	1.66
Leptolaimus	2.33	2.35	*Cyatholaimus*	2.00	2.01	*Diplopeltoides*	1.67	1.59	*Diplopeltoides*	1.33	1.66
Diplopeltoides	2.33	2.35	*Actinonema*	1.67	1.68	*Amphidless gen nov*	1.33	1.27	*Anoplostoma?*	1.00	1.24
Manganonema	2.33	2.35	*Diplopeltoides*	1.67	1.68	*Thalassironus*	1.00	0.96	*Diplopeltula*	1.00	1.24
Xyalidae	2.33'	2.35	*Quadricoma*	1.67	1.68	*Cervonema*	1.00	0.96			
Syringolaimus	2.00	2.01	*Amphimonhystera*	1.67	1.68	*Disconema*	1.00	0.96			
Tubolaimoides	2.00	2.01	*Syringolaimus*	1.33	1.34	*Paralinhomoeus?*	1.00	0.96			
Ascolaimus	2.00	2.01	*Phanodermopsis?*	1.00	1.01						
Desmoscolex	1.67	1.68	*Litinium*	1.00	1.01						
Quadricoma?	1.33	1.34	*Aegialoalaimus*	1.00	1.01						
Thalassironus	1.00	1.01	*Tubolaimoides*	1.00	1.01						
Oxystomina	1.00	1.01	*Daptonema*	1.00	1.01						
Cervonema	1.00	1.01									
Eudraconema	1.00	1.01									

Table 6.7 cont'd

9°N

0-1cm		%	1-2cm		%	2-3cm		%	3-5cm		%
Thalssomonhystera	29.67	30.58	*Syringolaimus*	22.00	27.50	*Thalssomonhystera*	29.67	28.43	*Syringolaimus*	39.67	40.48
Acantholaimus	5.33	5.50	*Thalssomonhystera*	20.00	25.00	*Syringolaimus*	24.33	23.32	*Thalssomonhystera*	22.67	23.13
Monhysteridae	5.33	5.50	*Acantholaimus*	4.33	5.42	*Diplopeltidae?*	7.33	7.03	*Acantholaimus*	3.67	3.74
Halalaimus	5.00	5.15	*Theristus*	3.67	4.58	*Acantholaimus*	4.33	4.15	*Cobbia*	3.33	3.40
Microlaimus	3.67	3.78	*Halalaimus*	3.00	3.75	*Theristus*	2.67	2.56	*Theristus*	2.67	2.72
Leptolaimus	3.67	3.78	*Manganonema*	2.67	3.33	*Linhystera*	2.33	2.24	*Halalaimus*	2.33	2.38
Desmoscolecidae	2.33	2.41	*Litinium*	2.00	2.50	*Camacolaimus*	2.00	1.92	*Manganonema*	2.33	2.38
Linhystera	2.33	2.41	*Desmoscolex*	2.00	2.50	*Manganonema*	2.00	1.92	*Diplopeltidae?*	2.33	2.38
Manganonema	2.33	2.41	*Leptolaimus*	1.33	1.67	*Halalaimus*	1.67	1.60	*Cyatholaimus*	2.00	2.04
Diplopeltula	2.33	2.41	*Cobbia*	1.33	1.67	*Diplopeltoides*	1.33	1.28	*Anoplostoma?*	1.33	1.36
Aegialoalaimus	2.00	2.06	*Campylaimus*	1.33	1.67	*Quadricoma*	1.33	1.28	*Leptolaimus*	1.33	1.36
Quadricoma	2.00	2.06	*Actinonema*	1.00	1.25	*Desmoscolex*	1.33	1.28	*Cyartonema*	1.33	1.36
Prochromadorella	1.67	1.72	*Chromadorella?*	1.00	1.25	*Paramonhystera?*	1.33	1.28	*Diplopeltoides*	1.00	1.02
Desmodora	1.67	1.72	*Cyatholaimus*	1.00	1.25	*Litinium*	1.00	0.96	*Desmoscolex*	1.00	1.02
Diplopeltoides	1.67	1.72	*Camacolaimus*	1.00	1.25	*Cervonema*	1.00	0.96	*Disconema*	1.00	1.02
Cobbia	1.67	1.72	*Amphidless gen nov*	1.00	1.25	*Cobbia*	1.00	0.96			
Syringolaimus	1.33	1.37	*Amphimonhystrella*	1.00	1.25	*Daptonema*	1.00	0.96			
Molgolaimus	1.33	1.37				*Diplopeltula*	1.00	0.96			
Xyalidae	1.33	1.37									
Nox	1.00	1.03									
Desmoscolex	1.00	1.03									
Amphimonhystera	1.00	1.03									
Linhomoeiidae?	1.00	1.03									

The distributions of the 10 most common species for each station at each depth interval are shown in figure 6.10. *Syringolaimus indet. juv.* increased in abundance with depth in the sediment at all stations. This was a very small nematode whose species identity was not discernible. *Cobbia sp. A* always reached its maximum abundance in the 1-2cm sediment layer. No clear patterns were obvious amongst the other dominant species, however. Three *Thalassomonhystera* species were found at all three stations, but at different densities and attaining maximum density at different sediment depths at each station.

6.2.2.2 α (Within-habitat) Diversity for Vertical Sediment Profiles

Values for α diversity indices at each sediment depth at each station are shown in figure 6.11. Within a station, Shannon-Wiener index (H') values indicated a marked decrease in diversity with increasing depth in the sediment. Interestingly, when the same depth intervals for different stations were compared, diversity was lower at nearly all depth intervals with increasing latitude, although these differences were not significant. Within a station, Pielou's J' also showed a drop in evenness with increasing sediment depth and similarly, at the same depth for different stations, evenness was lower at all depth intervals with increasing latitude. The 3-5cm layer was the exception to this general rule; at 9°N, both H' and J' were greater than at 5°N. These changes in H' and J' were not significant, however. It is also important to remember that the sharp drop in abundance with depth in the sediment will markedly influence values of H' and J'.

Composite rarefaction curves (Figure 6.12) were slightly different to other univariate measures, when the same sediment depths were compared along the latitudinal transect. The discrepancy with the other univariate measures probably occurred as a result of rarefaction estimates being sample-size independent. Below the 2cm horizon, biodiversity was least at 5°N. In the 1-2cm layer, biodiversity was highest at 5°N, although the curve follows that of the equatorial samples quite closely. All curves became progressively less steep with increasing depth in the sediment.

Figure 6.10 (shown overleaf) Species distributions for the 10 most dominant species present in 0-5cm sediment layers. Mean station abundance (% of total individuals per sample) for each species at each sediment depth is shown on the y-axis. Error bars are ± 1s.e. (a) Equator, (b) 5°N and (c) 9°N.

Figure 6.10a

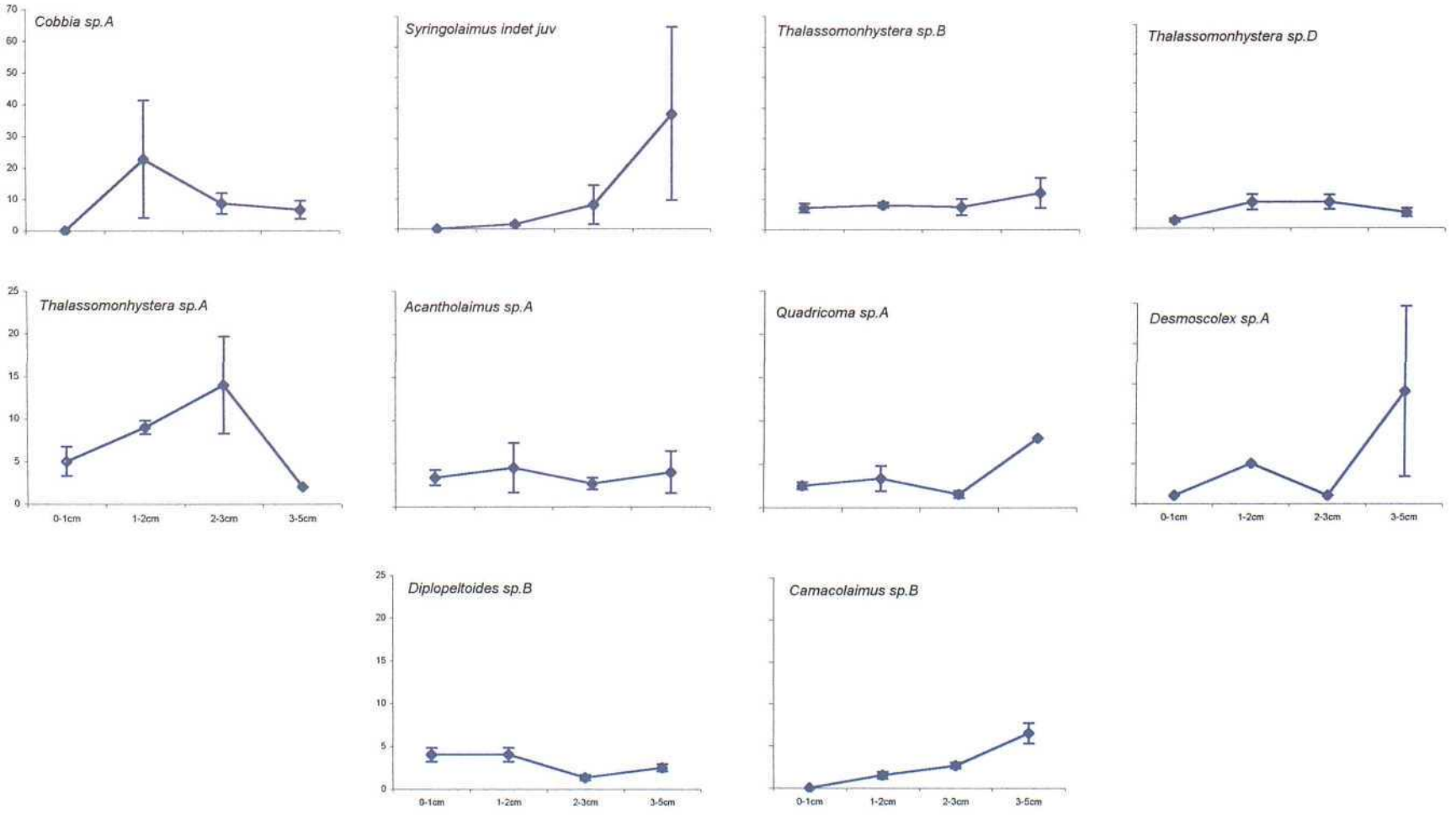

Cobbia sp.A
Syringolaimus indet juv
Thalassomonhystera sp.B
Thalassomonhystera sp.D
Thalassomonhystera sp.A
Acantholaimus sp.A
Quadricoma sp.A
Desmoscolex sp.A
Diplopeltoides sp.B
Camacolaimus sp.B
0-1cm
1-2cm
2-3cm
3-5cm

Figure 6.10b

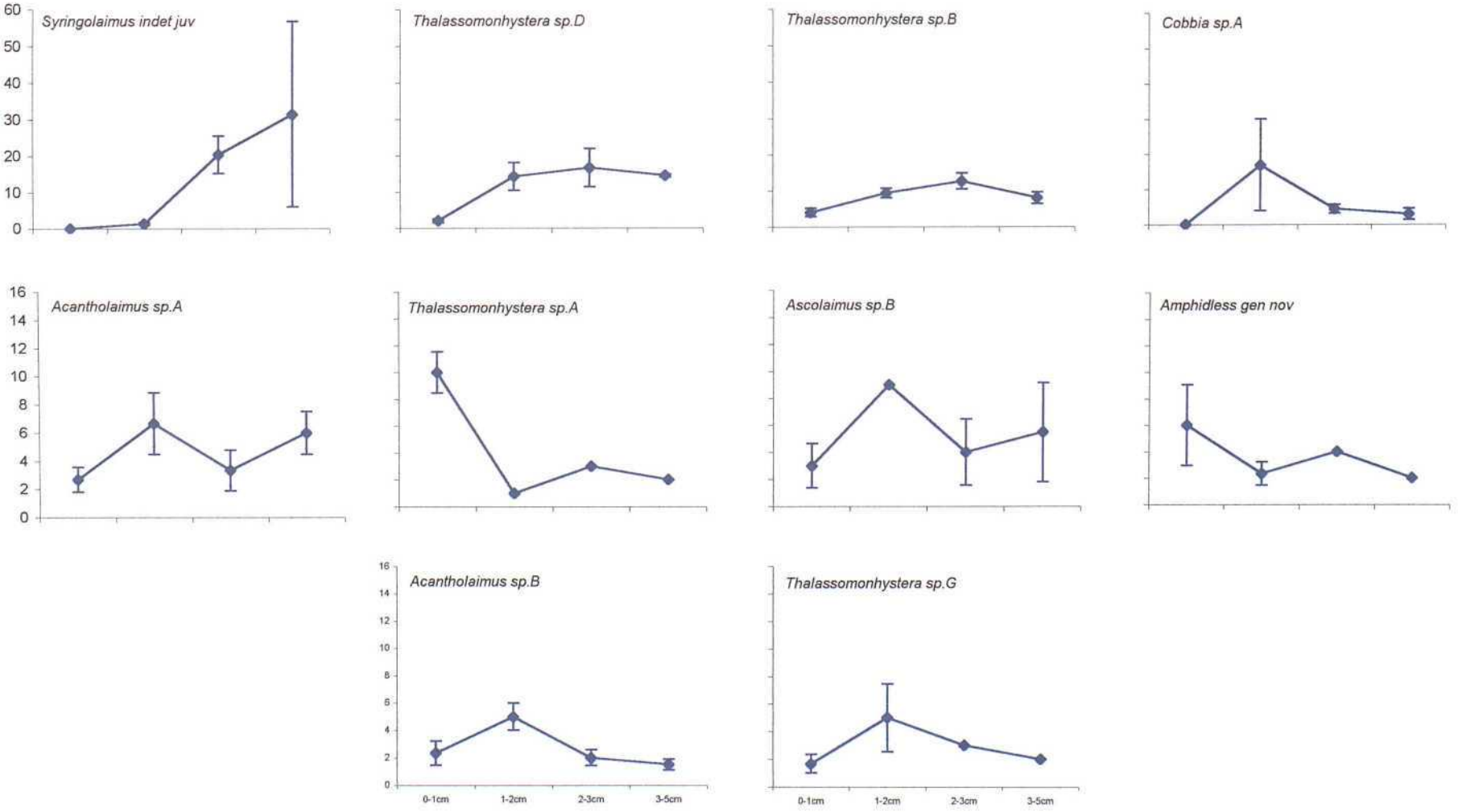

Syringolaimus indet juv
Thalassomonhystera sp.D
Thalassomonhystera sp.B
Cobbia sp.A
Acantholaimus sp.A
Thalassomonhystera sp.A
Ascolaimus sp.B
Amphidless gen nov
Acantholaimus sp.B
Thalassomonhystera sp.G
0-1cm
1-2cm
2-3cm
3-5cm

Figure 6.10c

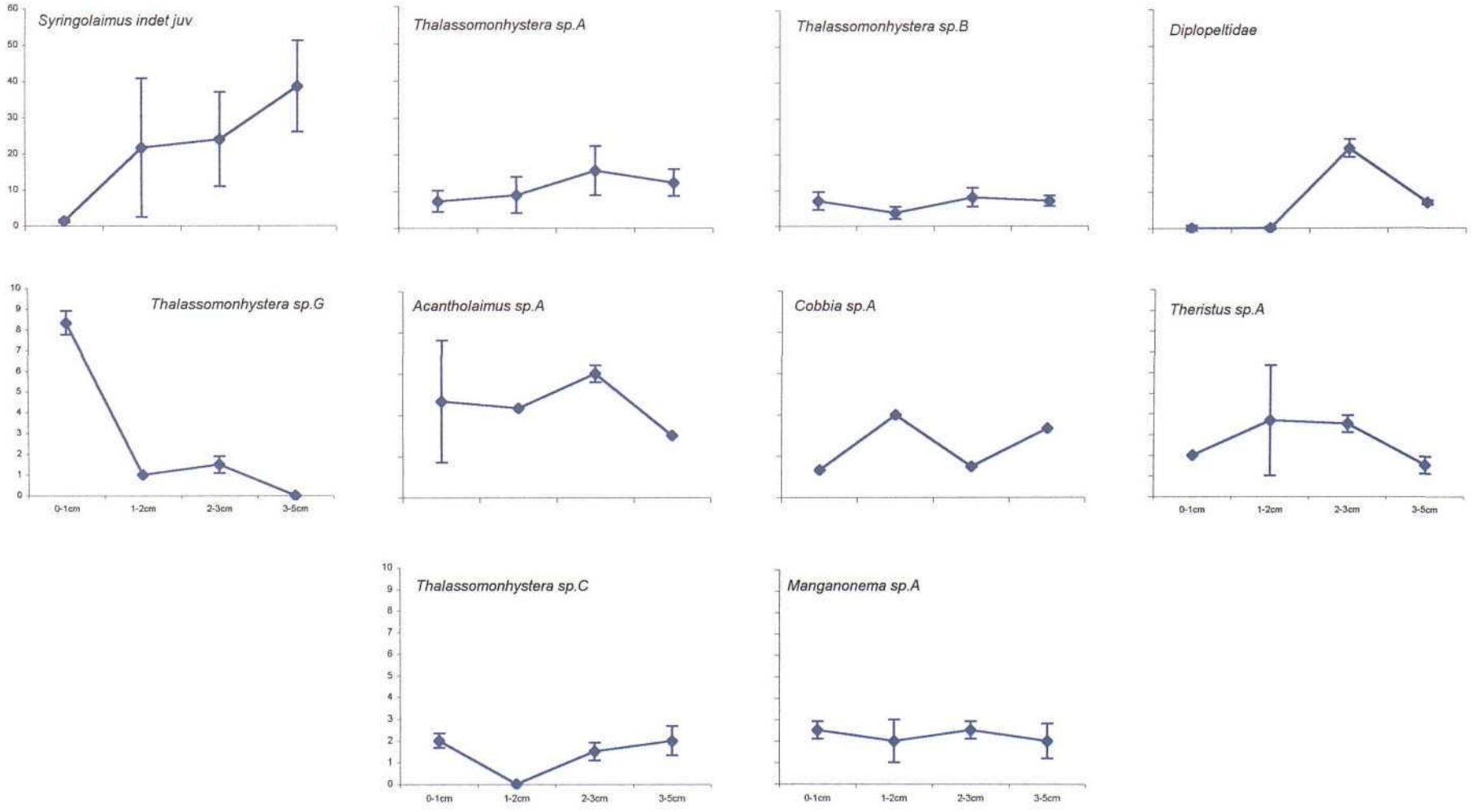

Syringolaimus indet juv
Thalassomonhystera sp.A
Thalassomonhystera sp.B
Diplopeltidae
Thalassomonhystera sp.G
Acantholaimus sp.A
Cobbia sp.A
Theristus sp.A
Thalassomonhystera sp.C
Manganonema sp.A
0-1cm
1-2cm
2-3cm
3-5cm

Figure 6.11 Mean α diversity values for each station (0, 5 and 9°N) at each sediment depth (0-5cm). Error bars are ± 1s.e.

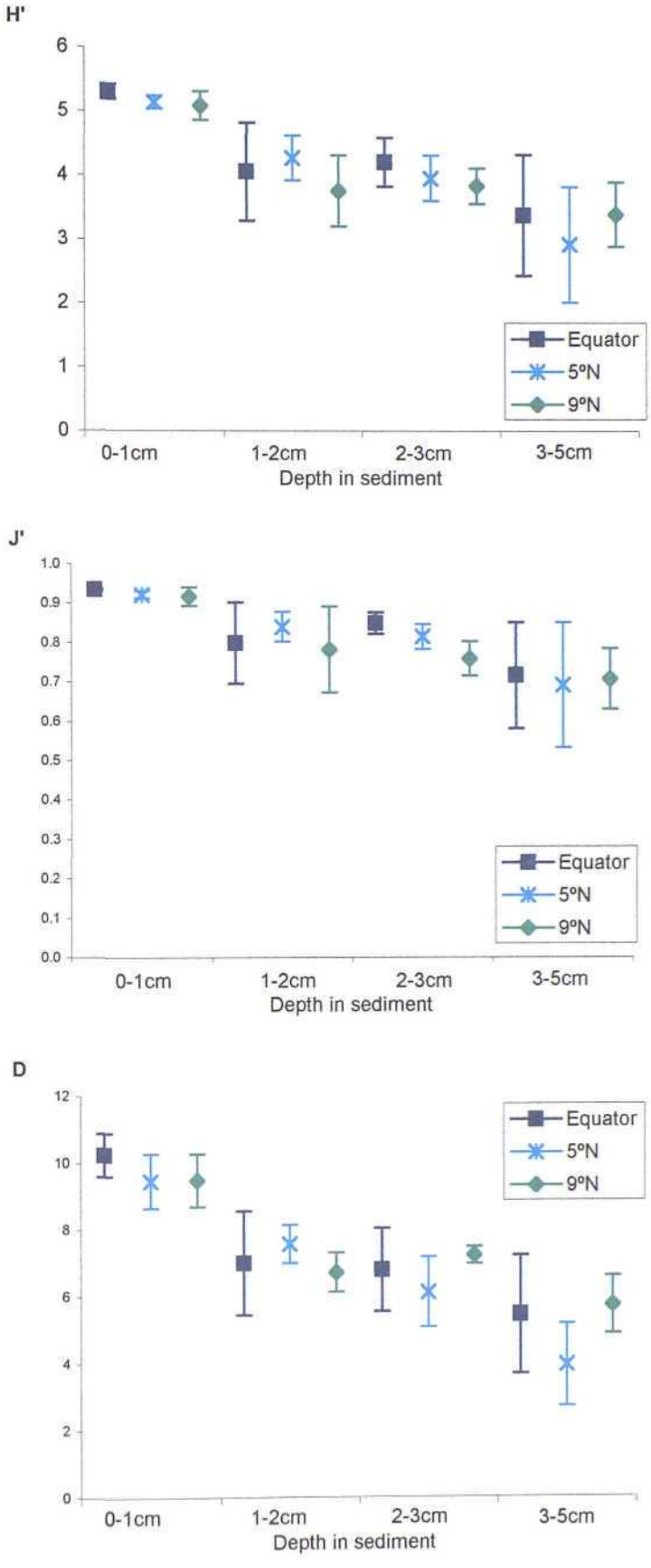
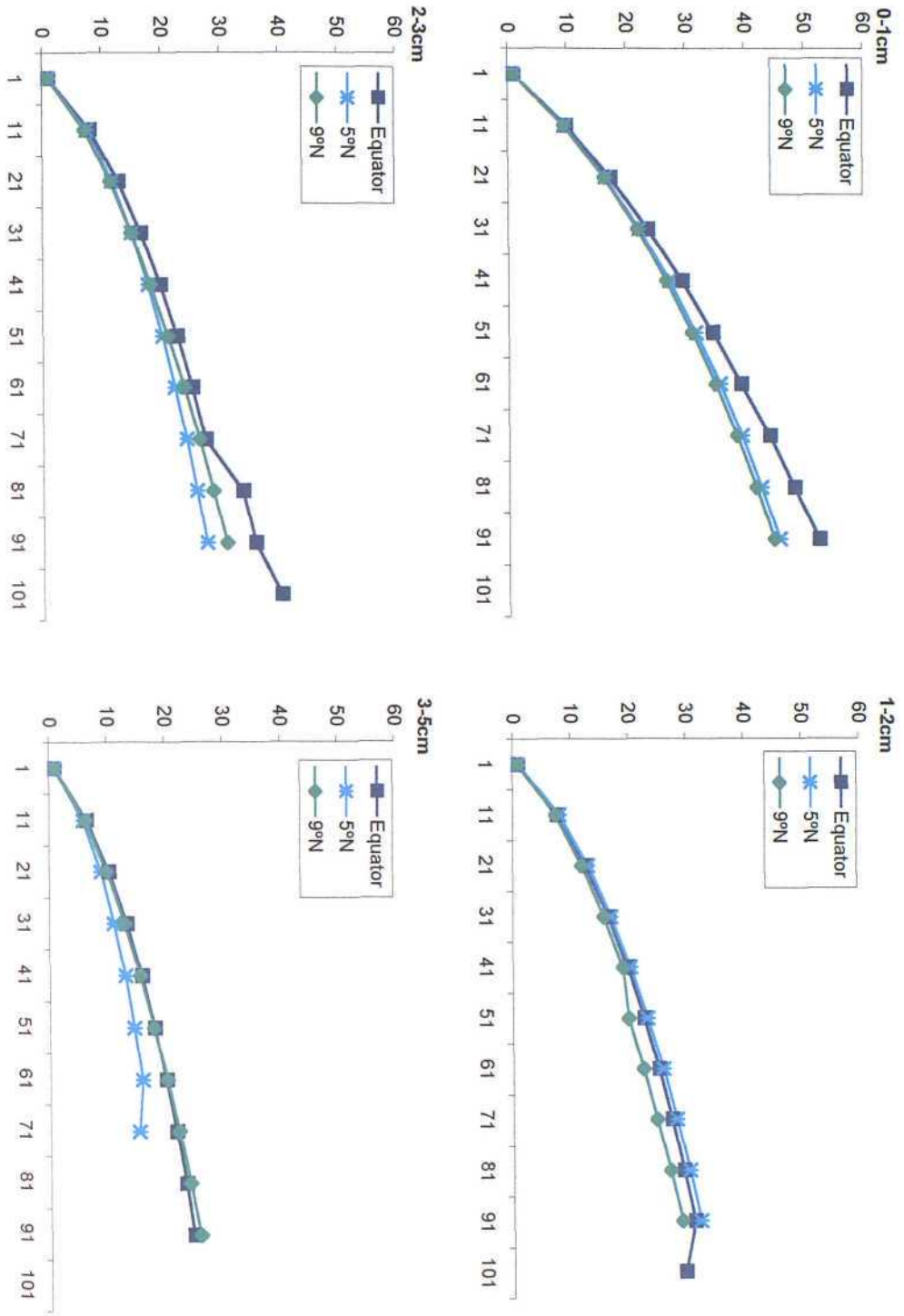


Figure 6.12 Mean rarefaction curves for each station (0, 5 and 9°N) at each sediment depth (0-5cm).



6.3 Discussion

The nematode communities of the abyssal equatorial Pacific were strongly dominated by species belonging to the Monhysteridae, Chromadoridae, Microlaimidae, Xyalidae and Oxystominidae families. These families are common to all deep-sea sites previously examined. In a study of abyssal communities in the southern Bay of Biscay, NE Atlantic (Dinet and Vivier, 1979), the dominant families were the Xyalidae and the Chromadoridae, followed by the Oxystominidae, Desmoscolecidae and Microlaimidae. In the West Atlantic there have been a number of detailed taxonomic studies; in the Venezuela Basin (Tietjen, 1984), the Hatteras Plain (Tietjen, 1989) and from the HEBBLE site on the Scotian Rise (Thistle and Sherman, 1985). The Hatteras Plain assemblages were dominated by the Oxystominidae, Chromadoridae and Xyalidae (Tietjen, 1989), whereas 15° further south in the Venezuela Basin, in addition to high abundance of the Desmoscolecidae, the Chromadoridae are replaced by Desmodoridae (Tietjen, 1984). The HEBBLE fauna are dominated, in order, by the Chromadoridae, Xyalidae, Oxystominidae and Sphaerolaimidae (Thistle and Sherman, 1985). One possible reason for the absence of the Microlaimidae and substitution of the Desmodoridae may be due to differences in the taxonomic placement of some members of the Microlaimidae. Lorenzen's (1981, in Lorenzen, 1994) schema, that was followed by Tietjen (1984; 1989), places *Molgolaimus* in the Desmodoridae instead of in the Microlaimidae, as in the current study. It seems that these widely separated areas, including the equatorial Pacific, show similarity in their faunal composition, at least at the family level.

An interesting pattern that did emerge in the equatorial Pacific, was the increasing abundance of members of the Xyalidae family with increasing latitude. The Xyalidae were a dominant family at 9 and 23°N, accounting for 13-18% of the total number of nematodes, but only up to 6% could be attributed to this family at stations at 0-5°N. It is hypothesised that this is related to the reduced availability of food at these more northerly sites. All sites of taxonomic study in the Atlantic receive similarly moderate levels of organic input, none are reported as receiving an input of phytodetritus, and the Xyalidae family is characteristically dominant at all of these sites (Dinet and Vivier, 1979; Tietjen, 1984; Thistle and Sherman, 1985; Tietjen, 1989), seemingly in agreement with this hypothesis.

Further confirmation of the hypothesis linking the Xyalidae to low-food areas is demonstrated in the distribution of the genus *Theristus*. This genus occurs frequently in the Atlantic samples and was a dominant genus at 23°N. However only one individual of this genus was found at the equatorial station and it was completely absent at 2 and 5°N in the 0-1cm sediment layer.

At the genus level, studies in the Atlantic have demonstrated dominance by five genera both in the east and the west Atlantic. These are *Theristus, Halalaimus, Desmoscolex* and *Acantholaimus/Spiliphera* (Dinet and Vivier, 1979; Tietjen, 1984; Thistle and Sherman, 1985; Tietjen, 1989). In the equatorial Pacific, *Thalassomonhystera* was the dominant genus at all stations and increased in abundance with increasing latitude. *Acantholaimus* and *Halalaimus* were also present in high numbers. *Microlaimus* and *Molgolaimus*, belonging to the Microlaimidae were common between the equator and 5°N, which is in contrast to studies in the Atlantic.

It is possible that the occurrence of microlaimid genera may be linked to phytodetritus deposition. None of the sites in the Atlantic where taxonomic studies have been made have been reported as receiving a phytodetrital input. Certainly in the equatorial Pacific samples, microlaimid genera decreased in importance with increasing latitude and additionally decreasing phytodetrital input. Thiel *et al.*. (1988/89) reported finding individuals belonging to the genus *Microlaimus* in detrital aggregates in samples collected at the BIOTRANS site in the north-eastern Atlantic. Furthermore, the feeding groups of Wieser (1953) places all microlaimids in the 2A category that Wieser (1953) suggested fed on epistrate organisms. This correlates well with the occurrence of high numbers of these nematode species in areas that had received inputs of intact diatoms and ciliates (Smith *et al.*, 1996).

Large numbers of a *Thalassomonhystera* species were also found within phytodetritus aggregates (Thiel *et al.*, 1988/89) at the BIOTRANS station, including juveniles belonging to larval stage 1 or 2. Riemann (1995) suggested that this indicated that reproduction was occurring inside the aggregates. A close relative of this species from shallow water can produce up to 23 generations per year (Vranken and Heip, 1986), suggesting that some *Thalassomonhystera* species may be capable of responding rapidly to take advantage of

such an ephemeral food source. In addition, small monhysterids such as these are very motile and can even swim short distances (Vranken *et al.*, 1981). This led Riemann (1995) to hypothesise that individuals may be able to disperse rapidly in response to the arrival of phytodetritus to the seafloor. These strategies are very characteristic of opportunistic species that are able to quickly take advantage of available resources. However, whilst this apparent association of some species of *Thalassomonhystera* with phytodetritus may explain the dominance of this genus at stations 0-5°N, it does not account for the increasing occurrence of some species of *Thalassomonhystera* at stations at 9-23°N.

According to Wieser (1959) and Tietjen (1976; 1984; 1989), species distribution can be related to sediment type and heterogeneity. At three different locations in the west Atlantic (Venezuela Basin, Hatteras Plain and off the North Carolina coast), a high proportion of the major genera were either restricted to or clearly most abundant in one specific sediment type. In the Venezuela Basin, abyssal sediment types were divided into pelagic, hemipelagic and turbidite sedimentary regimes which reflected discrete communities (Tietjen, 1984). The turbidite community was subsequently found to bear a greater resemblance to assemblages in the fine-grained turbidite sediments of the HEBBLE site on the Scotian rise (also abyssal), than with a second site in the Venezuela Basin where the sediments comprised poorly-sorted, heterogeneous material of pelagic origin (Thistle and Sherman, 1985). The sediments of the 0-5°N stations in the equatorial Pacific were calcareous foraminiferal sediments, which changed to very homogeneous fine-grained clays at 9 and 23°N (Berelson *et al.*, 1994; Stephens *et al.*, 1997). It is possible that the predominance of *Thalassomonhystera* at 9 and 23°N may be attributed to their preference for such a sedimentary regime rather than the absence of phytodetrital material or reduced POC flux.

Estimates of Shannon diversity (H') for the equatorial Pacific samples generally fell above those recorded for other deep-sea areas (Table 6.8) of comparable water depth and from the surface sediments. The only site where comparable values of H' have been recorded was in the Gulf of Biscay (Dinet and Vivier, 1979). Rather surprisingly, even the values of H' at stations at 9 and 23°N were higher than for sites in the Atlantic that have been assumed to receive a similar organic input (Tietjen, 1984; Jensen, 1988; Tietjen, 1989). Values for equitability (J'), however, did fall within the ranges previously recorded (Table

Table 6.8 Comparison of mean values of H'and J' for EqPac data and three abyssal locations in the Atlantic

	Equator	2°N	5°N	9°N	23°N	Bay of Biscay	Hatteras Plain	Venezuela Basin Pelagic	Venezuela Basin Hemipelagic	Venezuela Basin Turbidite	Norwegian Sea
Depth (m)	4309	4410	4411	4990	4879	4417	5411	3858	5054	3517	3178
H'	5.174	5.085	5.022	4.992	4.798	5.887	4.1	3.425	3.965	3.365	4.09
J'	0.935	0.934	0.923	0.918	0.894	0.936	0.87	0.93	0.955	0.85	0.865
Reference						Dinet and Vivier (1979)	Tietjen (1989	Tietjen (1984)	Tietjen (1984)	Tietjen (1984)	Jensen (1988)

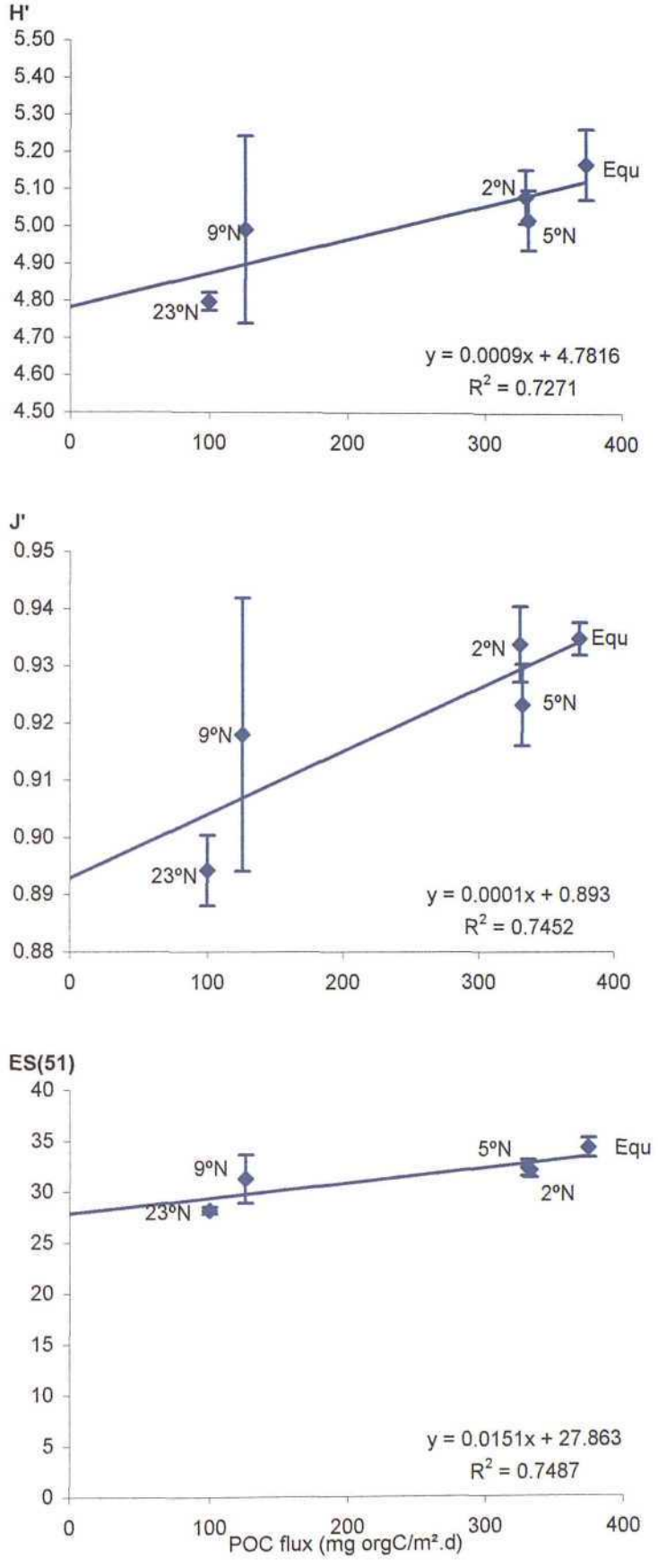
6.8). Values of J' from the stations at 0-5°N were encompassed in the values of equitability measured in pelagic and hemipelagic sediment communities in the Venezuela Basin (Tietjen, 1984). At 9 and 23°N, values of J' were most similar to those recorded from the Hatteras Plain (Tietjen, 1989), the Norwegian Sea (Jensen, 1988) and from turbidite sediments in the Venezuela Basin (Tietjen, 1984).

Etter and Grassle (1992) demonstrated that in the macrofauna, much of the variability in species diversity could be explained in terms of sediment heterogeneity. As already described in other chapters and earlier in this chapter, there is a noticeable change in sediment composition with a coincident drop in sediment heterogeneity between 5 and 9°N. If, as Etter and Grassle (1992) hypothesised, sediment diversity is 'controlling' species diversity in the EqPac nematode communities, a sharp transition in diversity would occur that was correlated to the observed change in sedimentary regime between 5 and 9°N. This clearly does not occur, instead diversity decreases almost linearly with increasing latitude.

Tietjen (1984) observed that species diversity of nematodes in the Venezuela Basin was directly related to proximity to areas of high surface productivity. He suggested that a higher organic input reduced competitive interactions thus allowing a richer fauna to develop. Subsequently, Grassle and Morse-Porteous (1987) and Grassle (1989) hypothesised that high diversity in the deep-sea benthos occurs as a result of small-scale disturbance acting on a low-productivity background, creating a spatial and temporal mosaic of patchy disequilibria. Grassle (1989) suggested that phytodetritus may act as a disturbance agent to enhance environmental heterogeneity as it settles into and around biogenic structures. This is not in agreement with the definition of disturbance used in the present study and consequently phytodetritus will be considered to be acting as an enrichment effect.

Paterson *et al.* (1998) could find no correlation between the species richness of abyssal polychaete assemblages and surface productivity at sites in the NE Atlantic and the eastern Pacific. In contradiction to these studies, nematode diversity and evenness in the abyssal, equatorial Pacific increased with decreasing latitude and, correspondingly, increasing POC flux (Figure 6.13). A high, positive correlation was obtained between annual POC flux and

Figure 6.13 Mean values for H', J' and ES(51) from the 0-1cm sediment layer along the US JGOFS transect correlated with annual POC flux (from Honjo *et al.*, 1995; Smith *et al.*, 1997). Error bars are ± 1s.e.

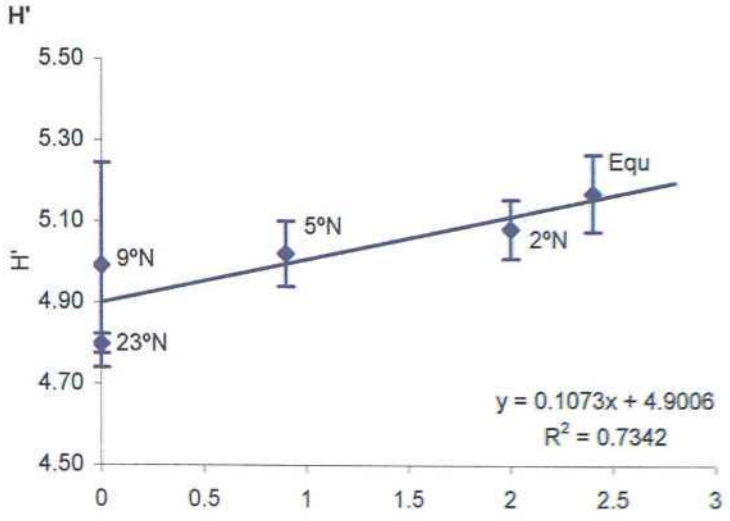


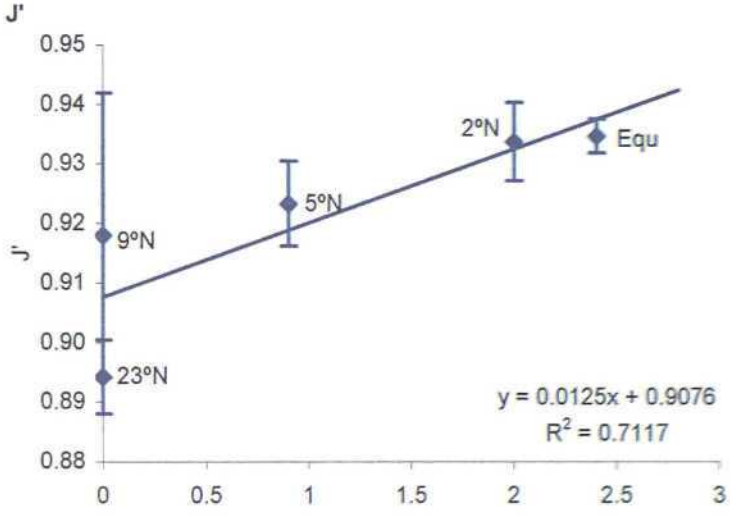
values of H' ($r = 0.857$, $P < 0.025$), J' ($r = 0.863$, $P < 0.025$) and species rarefaction diversity measured at $E(S_{51})$ ($r = 0.865$, $P < 0.025$). There was also a high, positive correlation between phytodetrital scores and values of H' ($r = 0.857$, $P < 0.025$), J' ($r = 0.844$, $P < 0.025$) and species rarefaction diversity measured at $E(S_{51})$ ($r = 0.808$, $P < 0.025$) (Figure 6.14).

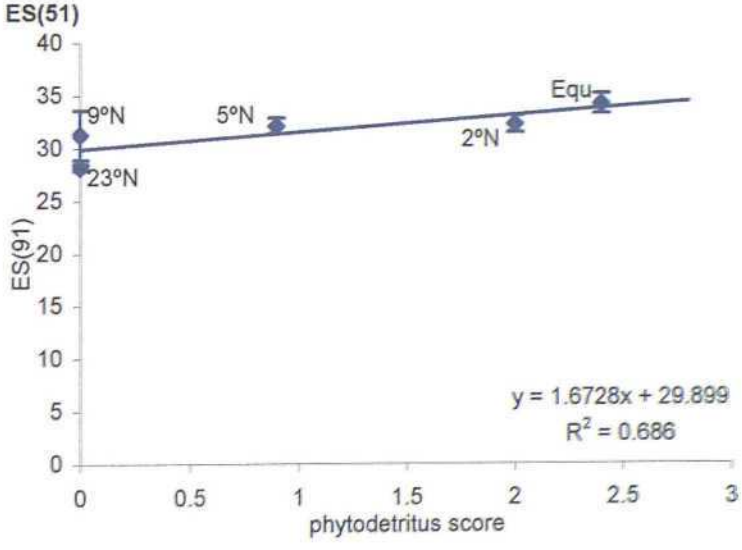
An examination of local diversity measures with depth in the sediment indicated that species diversity and evenness were enhanced in the underlying sediments as well as in the surface (0-1cm) sediment layer. At all sediment depths, values of H' and J' were greatest at the equator and then decreased with increasing latitude. Only one exception was apparent in the EqPac nematode communities; at 5°N diversity and evenness are lower than at 9°N below the 2cm sediment horizon. 5°N may have received a pulse of particulate organic carbon during the five months prior to benthic sampling that triggered an increase in biomass in the 0-1cm sediment layer and corresponding upwards migration of a few large individuals. It is proposed that this may have been responsible for the measured drop in diversity and evenness in the deeper sediment layers.

Bioturbation effects by larger animals have been documented by Smith *et al.* (1986) as acting as disturbance events in the deep sea. Mesocosm studies in shallow water have indicated that macrofauna have a significant impact on nematode diversity and equitability (Austen *et al.*, in press). The abundance of macrofauna between the equator and 2°N was found to be the highest ever recorded for abyssal sediments (Smith *et al.*, 1997). Megafaunal standing stocks were also greatest at the equator and were comprised predominately of burrowing urchins and mobile holothurians that are deposit feeders (Hoover *et al.*, 1994; Smith *et al.*, 1997). In addition to a physical disturbance effect, the megafauna in particular may have a secondary effect on nematode diversity. Burrows and other migratory tracks collect and concentrate phytodetrital aggregates which contribute to the patchiness of the organic input (Grassle and Morse-Porteous, 1987; Grassle, 1989) and may enhance local nematode diversity. This conflicts with the results of the functional group analysis which suggested that the trophic structure of the nematode communities, as revealed by morphological functional groups, was not affected by an increased abundance of larger organisms. However, diversity of the nematode assemblages in the equatorial Pacific appeared to be enhanced by reduced dominance of some species and increased

Figure 6.14 (shown overleaf) Mean values for H', J' and ES(51) from the 0-1cm sediment layer along the US JGOFS transect correlated with mean phytodetritus scores (from Smith *et al.*, 1996). Error bars are ± 1s.e. The mean phytodetritus score was based upon the visual inspection of multiple cores collected along the transect as follows: 0 = no visible flocculent material on core top, 1 = small amount (0-10% cover) of greenish material on top, 2 = substantial amount (10-90% cover) of greenish flocculent material, 3 = essentially complete cover of sediment-water interface (taken from Smith *et al.*, 1996).


H'
5.50
5.30
5.10
4.90
4.70
4.50
H'
9°N
5°N
2°N
Equ
23°N
y = 0.1073x + 4.9006
R² = 0.7342
0
0.5
1
1.5
2
2.5
3


J'
0.95
0.94
0.93
0.92
0.91
0.90
0.89
0.88
J'
9°N
5°N
2°N
Equ
23°N
y = 0.0125x + 0.9076
R² = 0.7117
0
0.5
1
1.5
2
2.5
3


ES(51)
40
35
30
25
20
15
10
5
0
ES(91)
9°N
5°N
2°N
Equ
23°N
y = 1.6728x + 29.899
R² = 0.686
0
0.5
1
1.5
2
2.5
3
phytodetritus score

occurrence of rarer species, i.e. increased evenness. It is suggested that the reason for the contrasting results reflects this shift in evenness, that would not be expected to significantly alter the functional group composition.

Grassle and Maciolek (1992) suggested that, as a result of the absence of barriers to dispersal and immigration in the deep sea, local species diversity is less influenced by species interactions and more by the regional species pool and rates of species recruitment to an area. Species richness curves plotted for the 0-1cm layer samples do not indicate that an asymptote was reached at any station, with the exception of 23°N. This suggests that the samples examined in this study do not adequately represent the regional species pool for each area along the transect. What is clear, however, is that species richness is greatest at the equatorial station. No comparison can be made of the species richness at stations 2-9°N as the curve for 9°N crosses that of the other two stations but 23°N has the lowest species richness.

The results of the cluster and NMDS analyses indicate that, at stations from 0-5°N, the nematodes were characterised by a discrete species pool, although they do display a greater affinity with each other than with the species pool at 9-23°N. Stations 9 and 23°N, on the other hand, were quite similar in terms of species composition. Annual POC flux (Honjo *et al.*, 1995; Smith *et al.*, 1997), microbial biomass (Smith *et al.*, 1997) and latitude were subsequently superimposed upon sample positions on the NMDS plot (Figure 6.15, 6.16 and 6.17). Annual POC flux seemed to best explain the location of the clusters on the plots for both untransformed and √√-transformed data, particularly for stations at 0-9°N.

The division of stations into two groups, 0-5°N and 9-23°N on the NMDS plots suggests that there are characteristic phytodetrital or elevated POC flux populations within the nematode communities. Similar populations were recorded for Foraminfera in phytodetrital aggregates in the Porcupine Seabight, NE Atlantic (Gooday and Lambshead, 1989). It is thought that there are several ways in which such assemblages may arise (Varon and Thistle, 1988). Firstly, higher rates of dispersion by certain species such as *Thalassomonhystera*, some microlaimids and chromadorids, into the phytodetrital material itself may generate a disproportionate abundance of these species in a habitat that was

Figure 6.15 NMDS results for data for 0-1cm sediment layer at all stations based upon comparisons of species lists, with superimposed annual POC flux into sediment traps, at each station (from Honjo *et al.*, 1995; Smith *et al.*, 1997). (a) untransformed data and (b) double-root (√√) -transformed data.

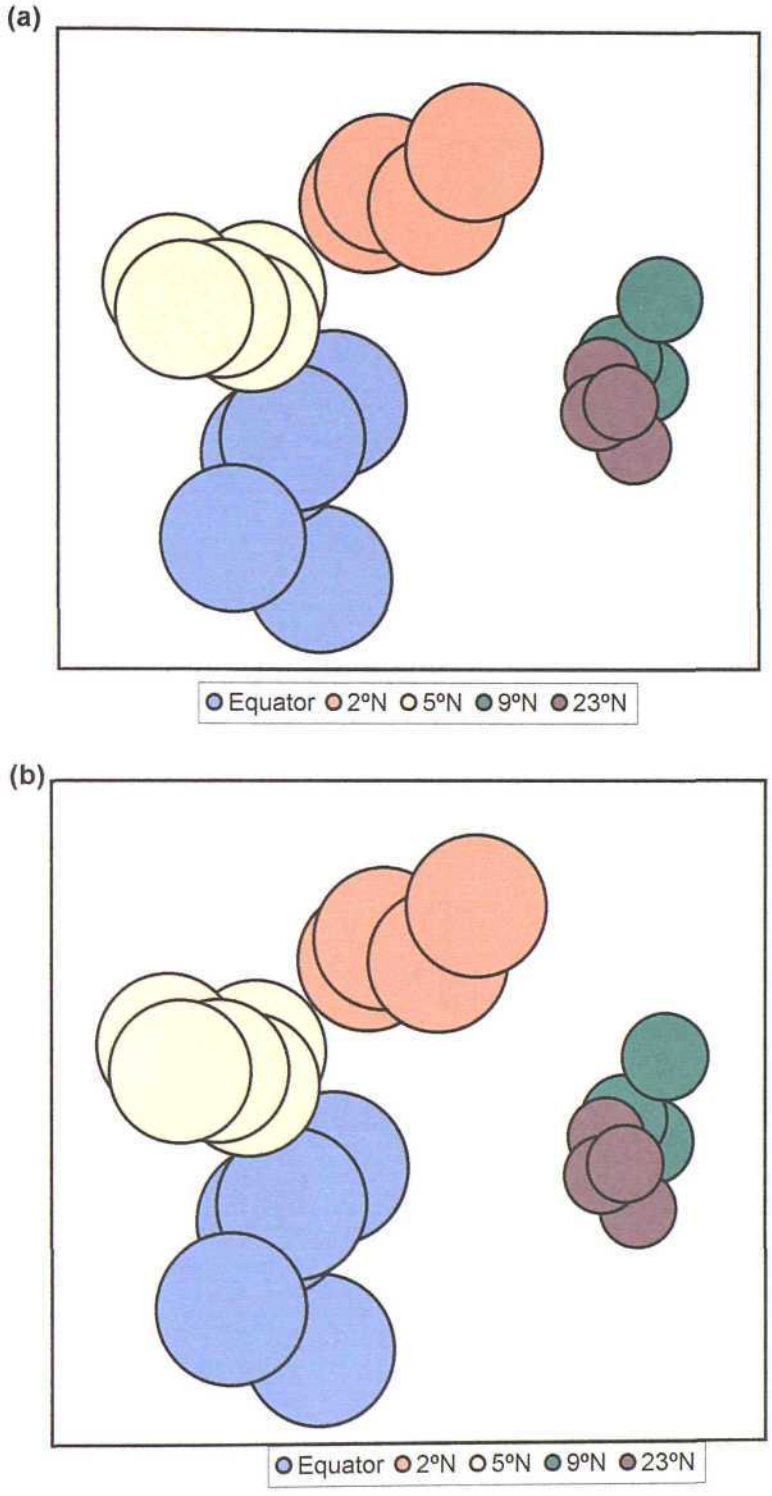


Figure 6.16 NMDS results for data for 0-1cm sediment layer at all stations based upon comparisons of species lists, with microbial biomass at each station superimposed (from Smith *et al.*, 1997). (a) untransformed data and (b) √√-transformed data.

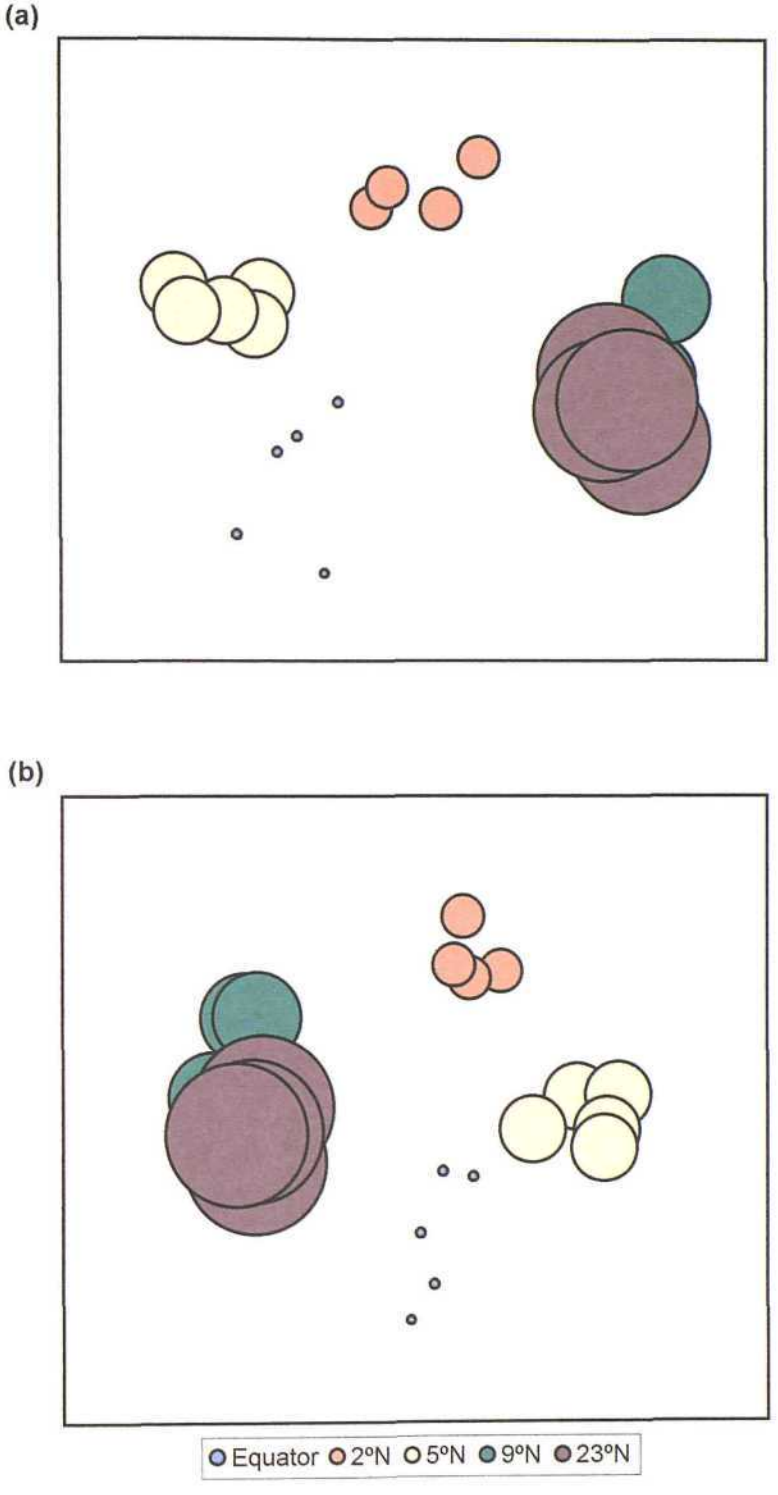
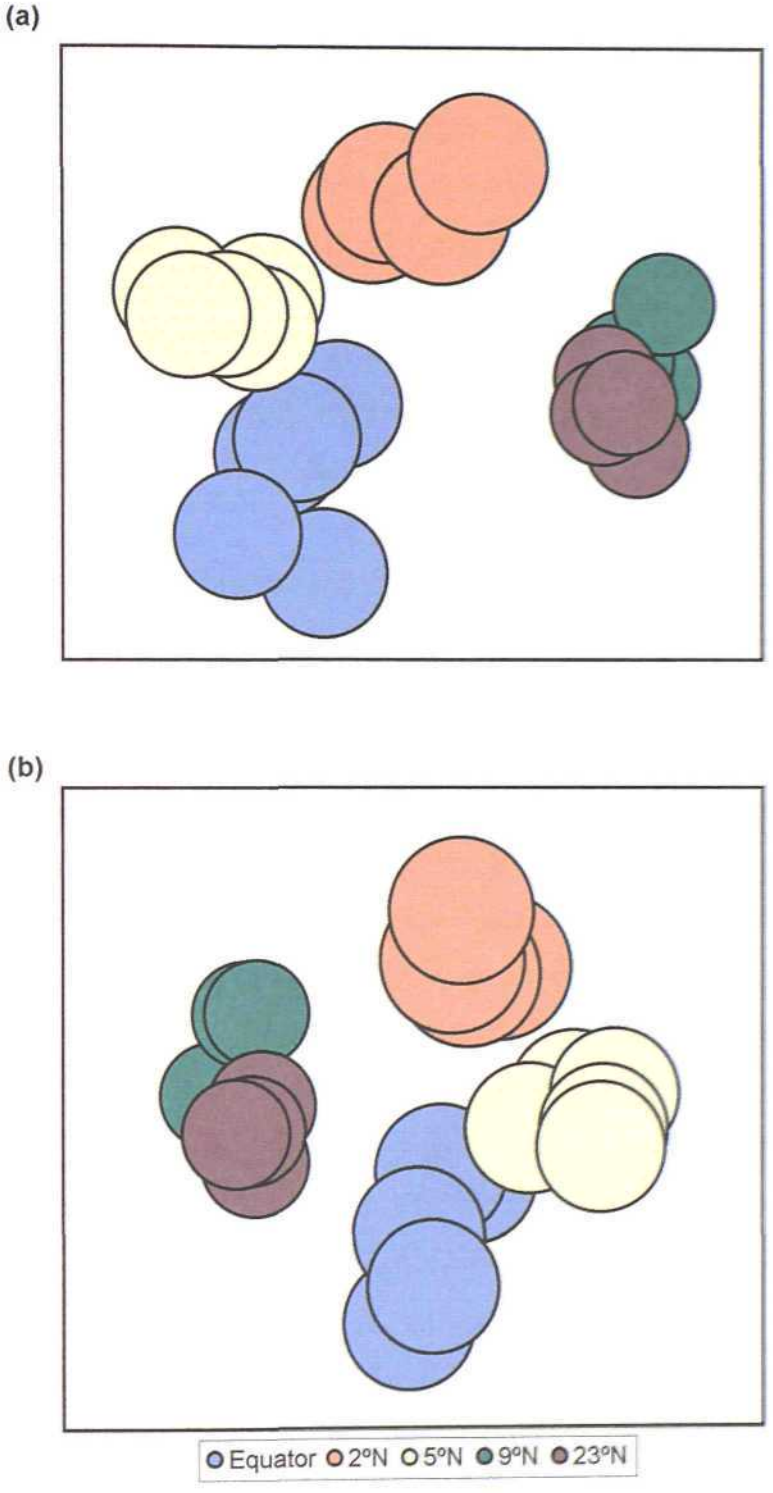


Figure 6.17 NMDS results for data for 0-1cm sediment layer at all stations based upon comparisons of species data, with degrees latitude for each station superimposed. (a) untransformed data and (b) √√-transformed data.



initially devoid of nematodes. Secondly, these species may colonise the detritus to minimise competitive and predatory interactions. Thirdly, they may be attracted to the detritus because it is an attractive food source. Only the second and third factors involve an active response by the nematodes to the phytodetritus (Varon and Thistle, 1988).

Within the nematode communities at 0-5°N, the monhysterids which dominate are thought to be examples of extreme opportunists that rapidly colonise and exploit newly-created patches (Bongers *et al.*, 1991), which, in this case, could be patches of phytodetritus. In shallow water they can reproduce very rapidly to quickly utilise new resources before the arrival of competing species. Gooday and Turley (1990) and Riemann (1995) invoked release from competition to explain rapid colonisation of phytodetrital aggregates by small monhysterids and chromadorids at the BIOTRANS site in the NE Atlantic. However, a response by opportunists generally produces a drop in diversity and evenness, in contrast to the increase measured in the EqPac data.

The increase in diversity and evenness that was recorded for the nematode communities at 0-5°N, may instead be attributable to a phytodetrital response by a number of species that are not abundant in background communities. Grassle and Maciolek (1992) have commented on the occurrence of "rare species that live only in association with such ephemeral resources" in the deep sea. These species may occur in densities so low in the background fauna that they are not recorded, even in an extensive sampling programme. Examples of a response by resource-associated macrofauna species were described by Turner (1973, 1977) for colonisers of experimentally-deployed wood panels that were unknown from background samples, and Smith *et al.* (1998) described the occurrence of seven exotic infaunal species in the sediments surrounding a whale skeleton in the Santa Catalina Basin, one of which was new to science. Both study areas had been sampled extensively prior to patch formation (Smith, 1985b; Smith, 1986; Grassle and Morse-Porteous, 1987). The absence of many dominant 0-5°N species and reduced abundance of others at the 9-23°N stations would be in agreement with this hypothesis. Evenness would be enhanced by an increase in the abundance of these rare species in response to elevated POC flux and/or phytodetritus as demonstrated in the present study.

6.4 Conclusions

- In the abyssal, equatorial Pacific, phytodetritus and elevated POC flux were correlated with an increase in nematode diversity, equitability and species richness in contrast to previous marofaunal studies (Paterson *et al.*, 1998) and studies of Foraminifera (Gooday *et al.*, 1998). This suggests that macro- and metazoan meiofauna are decoupled in their phytodetrital response.

- Phytodetritus and elevated POC flux were correlated with a change in nematode species composition, that was expressed at all stations from 0-5°N that receive a greater POC flux.

- There was some evidence observed to suggest that increased abundance of megafaunal organisms increased nematode diversity. Bioturbation effects by these organisms was expected to increase sediment heterogeneity due to rapid vertical mixing of phytodetritus and its associated microbial community. An increase in nematode diversity was observed within the depth of influence of these animals.

7.1 Introduction

On a small, localised scale, the monotonous expanses of the abyssal plain become characterised by high spatial heterogeneity or 'patchiness'. Much of this heterogeneity occurs at the scale of biological influence (such as locomotory range or the spread of feeding tentacles in macrofauna), and biogenic structures such as tubes, burrows and mounds may also be implicated in providing additional habitat complexity (Thistle, 1983; Smith *et al.*, 1986). Other components of habitat complexity include sessile, projecting structures such as agglutinating Foraminfera (Thistle, 1979) and the cirratulid 'mudballs' described by Jumars (1975). Such structures may provide refuge from predation, or resource-enriched habitats for small metazoans such as nematodes or other meiofauna (Gooday, 1984; Levin *et al.*, 1991b). Thistle and Eckman (1988) demonstrated the enhancing effect of such biogenic structures by placing mudball 'mimics' on the seabed. The abundance of some harpaticoid copepods was increased in or around them. In most cases these habitat islands attract aggregations of meiofaunal species.

Spatially and temporally patchy food supply may also be important. Deposition and current-driven resuspension of seasonal phytodetritus provide a small-scale heterogeneity that may persist for weeks or months (Rice and Lambshead, 1994). Lambshead and Gooday (1990) showed that patchiness of foraminiferal populations in the NE Atlantic increased following a phytodetrital input and the increase in nematode patchiness at the HEBBLE site was thought to reflect the release of resources not previously available, by benthic storms (Rice and Lambshead, 1994).

Grassle and Morse-Porteous (1987) suggested that patchiness acted to increase local diversity in their Spatio-temporal Mosaic Model. A habitat was said to consist of a number of patches, each at a different stage of recovery following a disturbance event. The species composition and diversity vary with time from disturbance, i.e., soon after recolonisation there is little competition for resources and diversity may be high. If disturbance does not recur, then eventually, some species will dominate and reduce diversity. At some

intermediate level or frequency of disturbance, the diversity of a habitat will be high, as many patches are not dominated by competitive dominants within the mosaic.

Grassle and Maciolek (1992) hypothesised the importance of these patches in maintaining high diversity over larger areas of the deep-sea floor. These patches may increase habitat heterogeneity on a small, localised scale and combined with a lack of barriers to dispersal act to maintain high regional diversity in deep-sea sediments.

It has been proposed that local diversity may be influenced by the mechanism of regional enrichment (Ricklefs, 1987; Ricklefs, 1989; Grassle and Maciolek, 1992; Cornell, 1993; Ricklefs and Schluter, 1993). In this regional enrichment model, local diversity represents a balance between local extinction and colonisation from the regional species pool, assuming that the pool of colonists is well mixed. Ricklef's model requires some special circumstances in order to predict correctly local diversity based upon regional diversity, such as very slow rates of competitive exclusion and frequent disturbances relative to these competitive exclusion times. Local extinction is considered to result from processes such as competition and predation, and physical disturbances that act to depress local diversity. As a consequence, local communities are thought to be undersaturated with respect to species (Cornell, 1993) and hence open to colonisation from the regional species pool. The size of the regional species pool is thought to be a function of the evolutionary history of speciation and adaptive radiation (Ricklefs, 1987). It is argued that, in accordance with the model, a larger regional species pool of colonists will, on average, support higher local diversities (Ricklefs and Schluter, 1993).

The regional enrichment model offers a convincing explanation for the higher local diversities observed by Rex *et al.* (1993) for some macrofaunal taxa at lower latitudes in the North Atlantic. Unlike the confined Norwegian Sea basin, there are more ecological opportunities for colonisation in the tropical Atlantic, simply as a consequence of its larger size and greater confluence with other ocean basins. Nutrient supply is more continuous and less variable than is experienced at higher latitudes (Yoder *et al.*, 1993), and there was an absence of catastrophic historic events such as glaciation or massive sedimentary flows, as occurred in the Norwegian Sea (Bugge *et al.*, 1988; Svavarsson *et al.*, 1993).

Consequently, as there are more opportunities for colonisation of the basin, the regional species pool would be expected to be more diverse.

Typically, the regional enrichment model has been tested by examining the relationship between local and regional diversity (see Stuart and Rex, 1994). A regression analysis, with local diversity as the response variable and regional diversity as an explanatory variable, found that nearly half of the variance in local diversity could be explained by regional diversity (Rex *et al.*, 1997). However, the underlying reasons for this inter-relationship are hard to discern. The model states that regional diversity augments local diversity by enrichment but it may simply reflect the accumulation of local diversities that are determined by small-scale processes. As Cornell (1993) stated, is the dependent variable local or regional diversity?

The diversity and trophic structure of EqPac communities were combined with the species database held at the Natural History Museum for a number of sites in the North Atlantic, and used to test the following hypothesis:

- Phytodetritus does not affect the biodiversity of nematode communities by enhancing the regional species pool.

7.2 Study Areas in the North Atlantic

The nematode species database held at the Natural History Museum (Department of Zoology), London, contains species lists for three stations that were used in the current study; the Porcupine Abyssal Plain (PAP) and the Madeira Abyssal Plain (MAP) in the NE Atlantic and the HEBBLE site in the NW Atlantic (Figure 7.1).

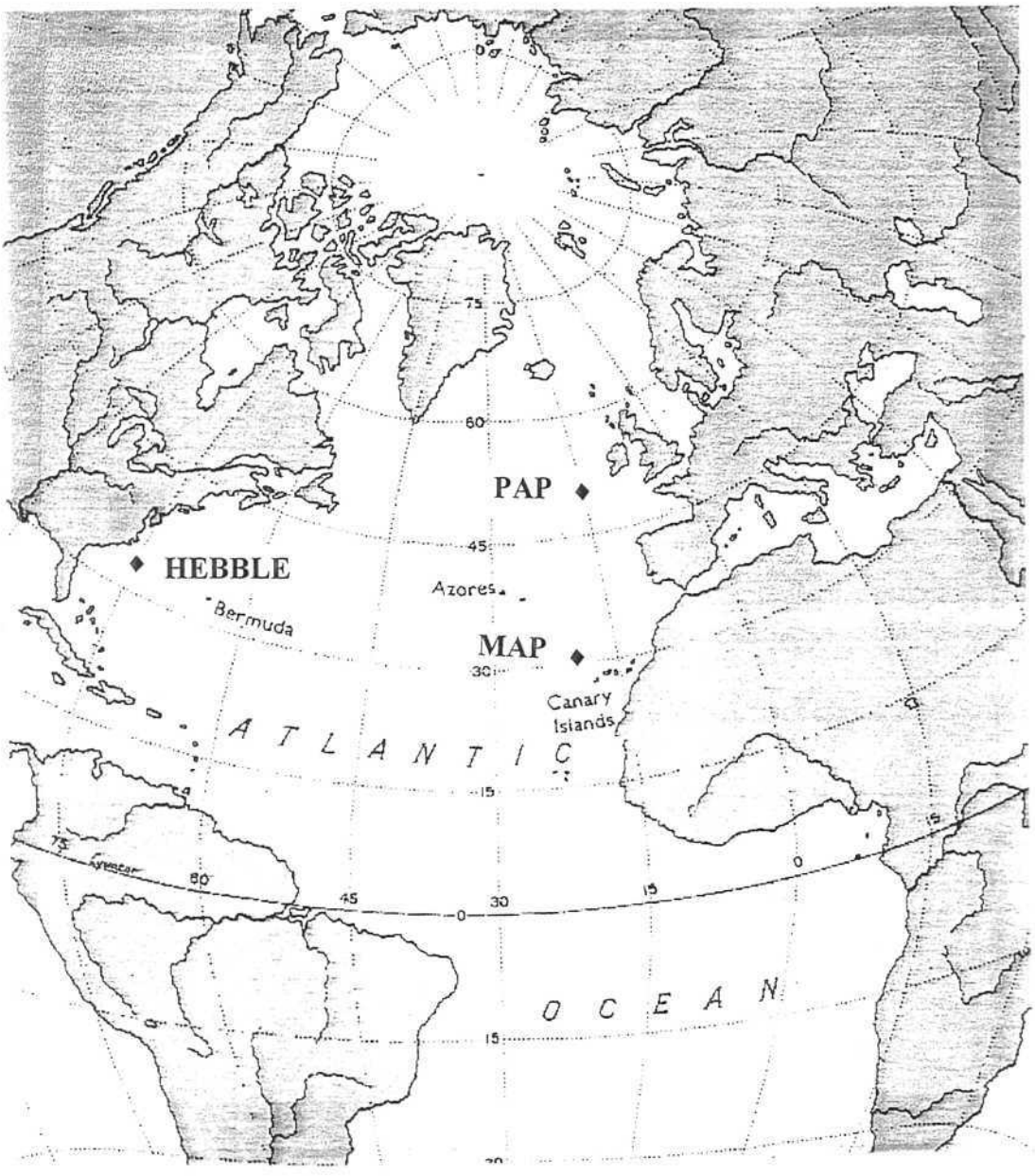
The two sites in the NE Atlantic were studied as part of a European Union Marine Science and Technology (MAST) multidisciplinary investigation into the effects of a seasonal flux of phytodetritus to the sea floor. PAP is located southwest of Ireland at 48° 50'N 16° 30'W at 4850m depth. This station receives a major seasonal input of phytodetritus (Lambshead *et al.*, 1994; Rice and Lambshead, 1994; Rice *et al.*, 1994). Samples were collected on two occasions at this location; the first occasion as part of the *RRS Discovery* cruise 185 during August-September, 1989, and the second as part of the *RRS Challenger* cruise 79 (May 1991).

The second station in the NE Atlantic (MAP) is located at 31° 05'N 21° 10'W at 4950m depth. This station was sampled during the *RRS Discovery* cruise 194 (August 1990). Time-series photographs have shown that MAP does not receive the major phytodetrital input experienced at PAP (Rice *et al.*, 1994). The two stations were chosen to differ as little as possible in terms of other variables, however.

At each station (including both time periods for PAP), one core (5.7cm internal diameter) was chosen from each of six multiple-core lowerings, a total of six samples. The top 0-1cm of sediment was fixed in buffered seawater formaldehyde solution (9:1 v:v), the nematodes extracted by the same Ludox decantation procedure used for the EqPac samples (45μm sieve) and mounted in glycerine on slides.

The HEBBLE site in the NW Atlantic is located at the foot of the Scotian Rise at 40°N 24'N 63° 08'W at 4626m depth. This was the location of preliminary studies for the High Energy Benthic Boundary Layer Experiment (Hollister and Nowell, 1991). Although evidence suggests an abundant food supply to the benthos (Hollister and Nowell, 1991), the sea floor is subjected to severe benthic storms, when maximum velocities 10m above

Figure 7.1 Map indicating the location of the North Atlantic sampling stations on the Porcupine Abyssal Plain (PAP), the Madeira Abyssal Plain (MAP) and at the site of the High Energy Benthic Boundary Layer Experiment (HEBBLE).



the sea bed can reach 15-40cm s^{-1} (Hollister and Nowell, 1991). During storms the surface sediment layer is eroded and subsequently redeposited during the quiescent inter-storm periods. Samples were collected using a USNEL box-corer and the nine central subcores, each with a sediment volume of 77cm^2 (Thistle *et al.*, 1995) were sampled for nematodes. Subcores from two box cores were examined. The top 0-1cm of sediment from each subcore was fixed in buffered seawater formalin (4:1 v:v) and a 25% random subsample of the nematodes was obtained using the method described in Sherman *et al.* (1984).

Table 7.1 contains a list of abiotic variables cited in the literature for all central Pacific sites, NE and NW Atlantic stations and also includes nematode abundance and biomass, where available.

Table 7.1 Comparison of abiotic variables noted in the literature for the stations in the equatorial Pacific, NE and NW Atlantic.

	Central Pacific					NE Atlantic		NW Atlantic
	Equator	2°N	5°N	9°N	23°N	PAP	MAP	HEBBLE
Average water depth (m)	4305	4411	4440	4990	4880	4845	4942	4820
Phytodetritus observed?	Yes - large aggregates with intact phytoplankters		Yes - green veneer	No	Yes - but much smaller quantities than at 0-5°N	Yes - large aggregates forming thick layer	No	No
DW POC flux (g C/m²/yr)	34.7	26.5	26.1	8.6	3.13	26.9	21.9	No data available
Sedimentary characteristics	*Coarse calcareous foraminiferal mud* mixed with fine buff muds			*Fine clays with some* mangnese nodules present		Soft, brown mud overlying sticky, cream coloured mud at approx. 23cm depth	Soft, buff grey sediment 5cm thick overlying coarser turbidite sediments	Soft, brown mud overlying coarse foraminiferal sediments
Hydrodynamic regime	Quiescent				Quiescent	Quiescent	Quiescent	Frequent, high energy benthic storms
Mean nematode abundance (no's.10cm²)	59.6	96.32	64.46	44.6	40.34	388.57	105.57	Data not available
Mean nematode biomass (µg.100cm²)	30.76	82.35	87.36	18.9	19.39	135.4	Data not available	Data not available
References	Berelson *et al*., 1995; Smith *et al*., 1996; Lampitt and Antia, 1997; Stephens *et al*., 1997				CR Smith, pers. obs.; Karl *et al*., 1996	AJ Gooday, pers. obs.; Lampitt, 1985; Rice *et al*., 1986; Vincx *et al*., 1994; Lambshead *et al*., 1995; Lampitt and Antia, 1997		Thistle and Sherman, 1985; Hollister and Nowell, 1991

7.3 Results

7.3.1 Comparisons of α (Within-habitat) Diversity

When values of Shannon , H', diversity were grouped, *a priori*, into stations that do receive an input of phytodetritus and stations that do not, H' diversity was significantly greater at those stations receiving phytodetritus ($P < 0.0005$, using a Mann-Whitney U-test). When values of H' were compared by station (Figure 7.2), a Kruskal-Wallis test indicated that a significant difference occurred between at least one pair of samples ($P < 0.0005$). Examination of the Z-values for each station showed that, in agreement with the *a priori* groupings, stations at the equator, 2 and 5°N were not significantly different from PAP1 or PAP2 but had significantly greater diversity than MAP or HEBBLE. Similarly, stations at 9 and 23°N were not significantly different from MAP and HEBBLE but were significantly different from PAP1 and PAP2 (Table 7.2). It is also interesting to note that the mean values of H' for the EqPac stations from 0-5°N fall between the values for PAP1 and PAP2.

A somewhat different pattern was observed for values of J' (Figure 7.2). When the stations were grouped *a priori* into with-phytodetritus and without-phytodetritus stations, evenness at stations receiving phytodetritus was not significantly different from evenness at stations that do not ($P = 0.2219$, using a Mann-Whitney U-test). When the values of J' were compared by station, there were no significant differences in evenness between PAP1, PAP2, HEBBLE and 23°N, and similarly there were no significant differences between MAP and the EqPac stations from 0-9°N (Table 7.3).

Rarefaction curves were plotted for each station and the curves for samples within a station were deemed to be similar enough that it was acceptable to take a mean value at each point. Mean rarefaction curves for all stations show that rarefaction diversity was highest at the equator (Figure 7.3). A group containing PAP2 and stations from 2-5°N that closely overlap had the next highest rarefaction diversity. A third group containing 23°N, PAP2, HEBBLE and MAP had the lowest diversity of the stations examined. The stations were normalised to $E(S_{51})$ and a Kruskal-Wallis test showed that PAP2 was not significantly different from stations at 0-9°N, and PAP1, MAP, HEBBLE and 23°N were

Figure 7.2 Mean α diversity values for 0-1cm sediment layer at all Pacific and Atlantic stations. PAP1 = first sampling event at the Porcupine Abyssal Plain, PAP2 = second sampling event at PAP, MAP = Madeira Abyssal Plain, HEBBLE = High Energy Benthic Boundary Layer Experiment. Error bars are ± 1s.e. (a) Shannon H' diversity and (b) Pielou's J' evenness.

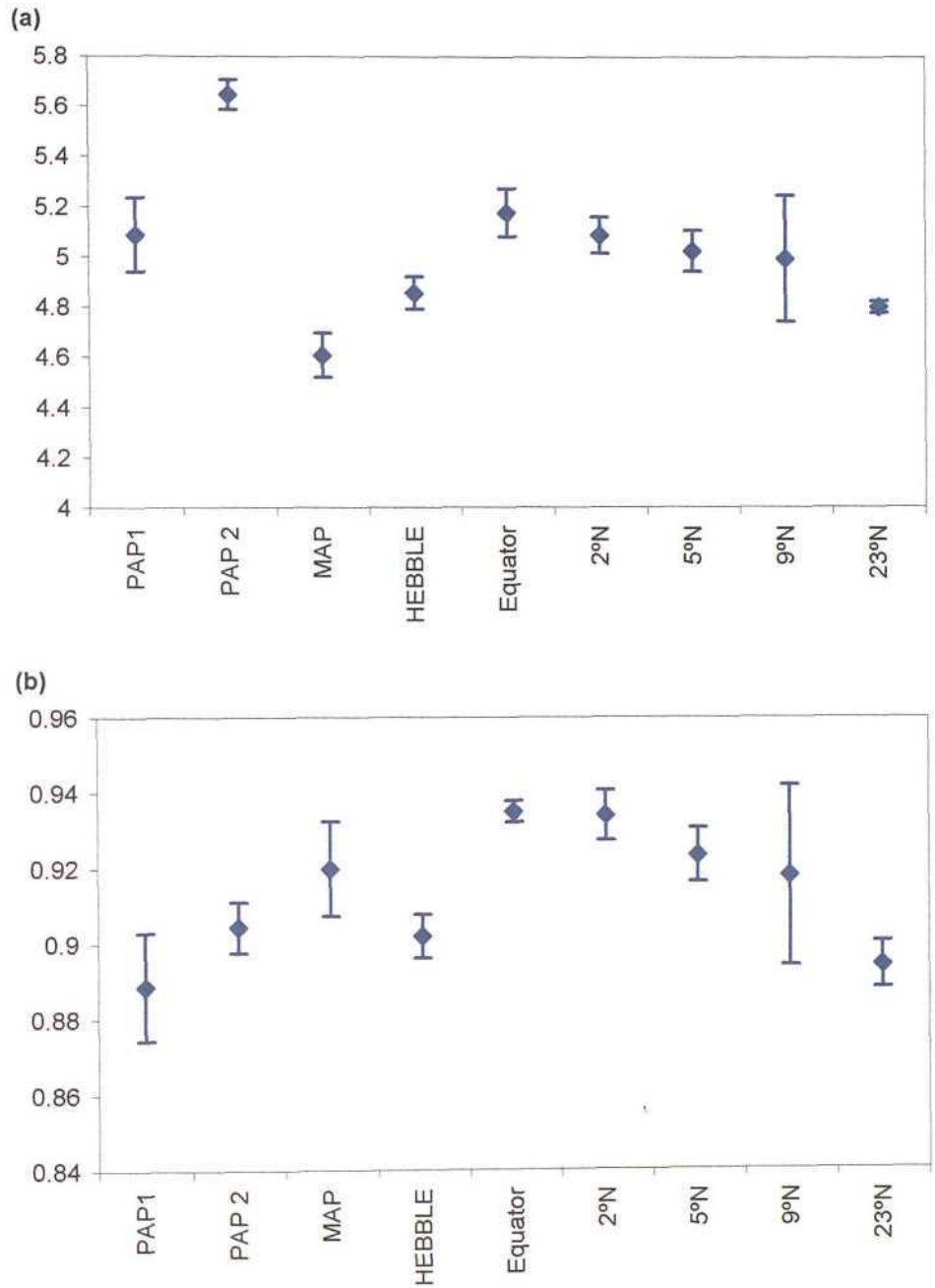


Table 7.2 Mean values of Shannon's H' (log-base 2) for four sites in the North Atlantic and five sites in the Pacific Ocean. Also shown are Kruskal-Wallis test statistic, Z, values.

	PAP1	PAP2	MAP	HEBBLE	Equ	2°N	5°N	9°N	23°N
	5.146	5.572	4.806	4.159	4.898	5.049	4.771	5.231	4.774
	5.158	5.84	4.867	4.287	5.371	4.899	4.973	4.489	4.754
	5.515	5.677	4.485	5.028	4.998	5.232	5.233	5.257	4.8
	5.322	5.412	4.641	5.008	5.337	5.161	5.161		4.865
	4.887	5.741	4.564	4.914	5.265		4.972		
	4.486	5.614	4.273	4.788					
				4.673					
				4.997					
				4.959					
				4.862					
				4.693					
				5.038					
				5.092					
				4.888					
				4.925					
				4.942					
				5.263					
Mean	5.08567	5.64267	4.606	4.85388	5.174	5.085	5.022	4.992	4.798
1s.e.	0.14698	0.06022	0.08881	0.06531	0.095	0.073	0.081	0.252	0.024
Z	0.62	3.43	-2.48	-1.22	1.21	1.59	1.27	-1.91	-2.72

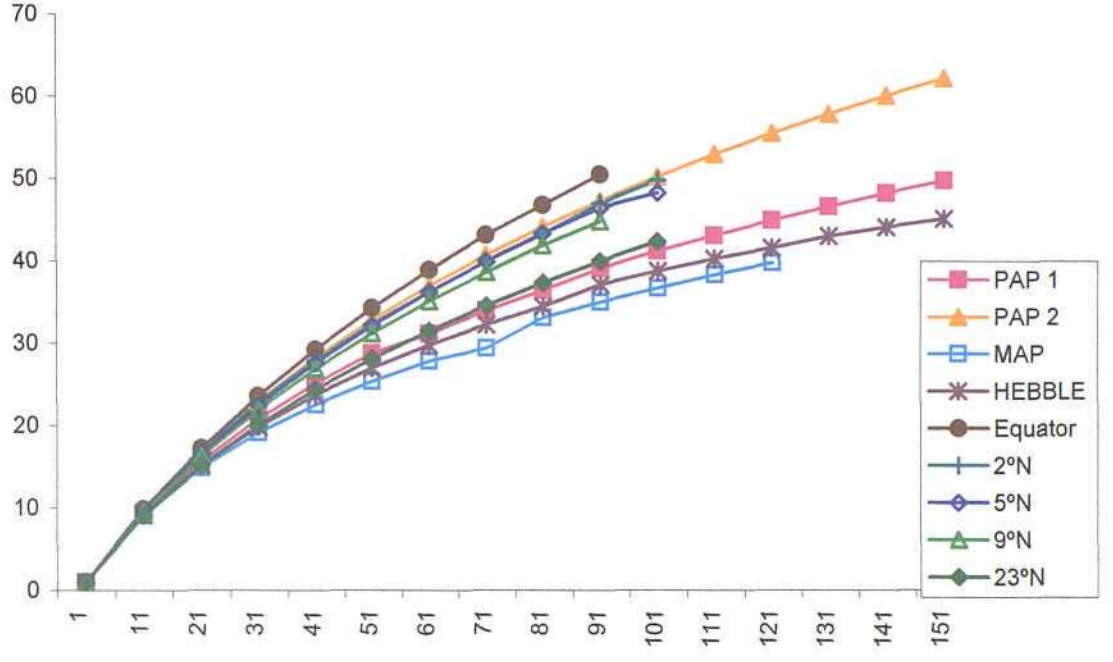
$P < 0.0005$

Table 7.3 Mean values of Pielou's J' (log-base n) for four sites in the North Atlantic and five sites in the Pacific Ocean. Also shown are Kruskal-Wallis test statistic, Z, values.

	PAP1	PAP2	MAP	HEBBLE	Equ	2°N	5°N	9°N	23°N
	0.864	0.886	0.903	0.896	0.938	0.927	0.904	0.934	0.902
	0.892	0.904	0.867	0.948	0.944	0.920	0.937	0.871	0.876
	0.897	0.914	0.943	0.932	0.929	0.950	0.926	0.949	0.902
	0.865	0.92	0.946	0.923	0.929	0.939	0.940		0.897
	0.953	0.919	0.94	0.9	0.935		0.910		
	0.861	0.883	0.92	0.9					
				0.846					
				0.9					
				0.908					
				0.88					
				0.865					
				0.907					
				0.889					
				0.918					
				0.925					
				0.895					
				0.902					
Mean	0.889	0.904	0.920	0.902	0.935	0.934	0.923	0.918	0.894
1s.e.	0.014	0.007	0.013	0.006	0.003	0.007	0.007	0.024	0.006
Z	-2.01	-0.75	1.15	-1.71	2.28	1.94	1.25	0.67	-1.45

$P = 0.013$

Figure 7.3 Mean rarefaction curves for 0-1cm sediment layer at all Pacific and Atlantic stations. See figure 7.2. for explanation of abbreviations used in legend.



not significantly different (Table 7.4). When the stations were grouped into stations that do and do not receive phytodetritus, there was a highly significant difference ($P < 0.0005$, using a Mann-Whitney U-test).

k dominance curves were plotted for each station and were deemed to be similar enough that it was acceptable to take a mean value for each point. The mean *k* dominance curves also indicated an increase in diversity for stations that do receive an input of phytodetritus (Figure 7.4). Diversity was greatest for PAP2, followed by the EqPac equatorial station, then stations at 2 and 5°N. The *k* dominance curve for PAP1 crosses those of the EqPac stations indicating that diversity at these stations cannot be adequately compared using univariate measures. This means that relative species diversity will depend upon which point upon the curves diversity is compared.

7.3.2 Comparisons of β (Between-habitat) Diversity

The β diversity measure of species richness indicated a different pattern of diversity than the α diversity measures (Figure 7.5). Species richness was greatest at PAP2 with some distance separating that curve from the collector's curves for the EqPac equatorial station and PAP1. The curves for the remaining EqPac stations indicated decreasing species richness with increasing latitude. The collector's curve for the HEBBLE samples lay between the curves for the EqPac stations at 9 and 23°N. MAP had the lowest species richness.

7.3.3 Comparison of Community Composition

The nematode community composition of the EqPac and NE Atlantic samples were compared at the genus level, using cluster analysis based upon the Bray-Curtis index of similarity. It was not possible to make a comparison at the species level due to the use of morphological species. These were defined by different workers and it was felt that while genera would have been accurately ascribed, particular species would not correlate. It is possible that in the future this problem may be overcome by the use of standardised data sets with pictorial keys that are available to all workers, perhaps by utilising the Internet as a means of communication. Furthermore, it has been demonstrated that assemblages may by analysed at the genus level with very little loss of information (Warwick, 1988;

Table 7.4 Mean values of E(S51) for four sites in the North Atlantic and five sites in the Pacific Ocean. Also shown are Kruskal-Wallis test statistic, Z, values.

	PAP1	PAP2	MAP	HEBBLE	Equ	2°N	5°N	9°N	23°N
	27.49	32.72	26.36	20.99	35.15	31.61	30.04	33.34	28.6
	27.96	34.04	25.7	0	35.83	30.66	31.94	26.58	28.16
	30.59	33.28	23.38	29.79	30.58	34.24	34.46	33.9	27.26
	28.55	31.91	26.18	27.18	34.61	33.03	33.16		28.72
	32	34.14	26.26	27.88	35.53		31.28		
	26.17	31.44	24.43	25.74					
				24.33					
				27.88					
				28.68					
				28.36					
				26.11					
				25.2					
				28.11					
				28.38					
				26.8					
				27.64					
				29.3					
Mean	28.7933	32.9217	25.385	27.0231	34.34	32.385	32.176	31.2733	28.185
1s.e.	0.87264	0.45177	0.49597	0.53053	0.96184	0.78705	0.76177	2.35223	0.331
Z	-0.53	2.52	-3.34	-3.32	3.15	1.78	1.88	0.82	-0.51

$P < 0.0005$

Figure 7.4 Mean *k* dominance curves for 0-1cm sediment layer at all Pacific and Atlantic stations. See figure 7.2. for explanation of abbreviations used in legend.

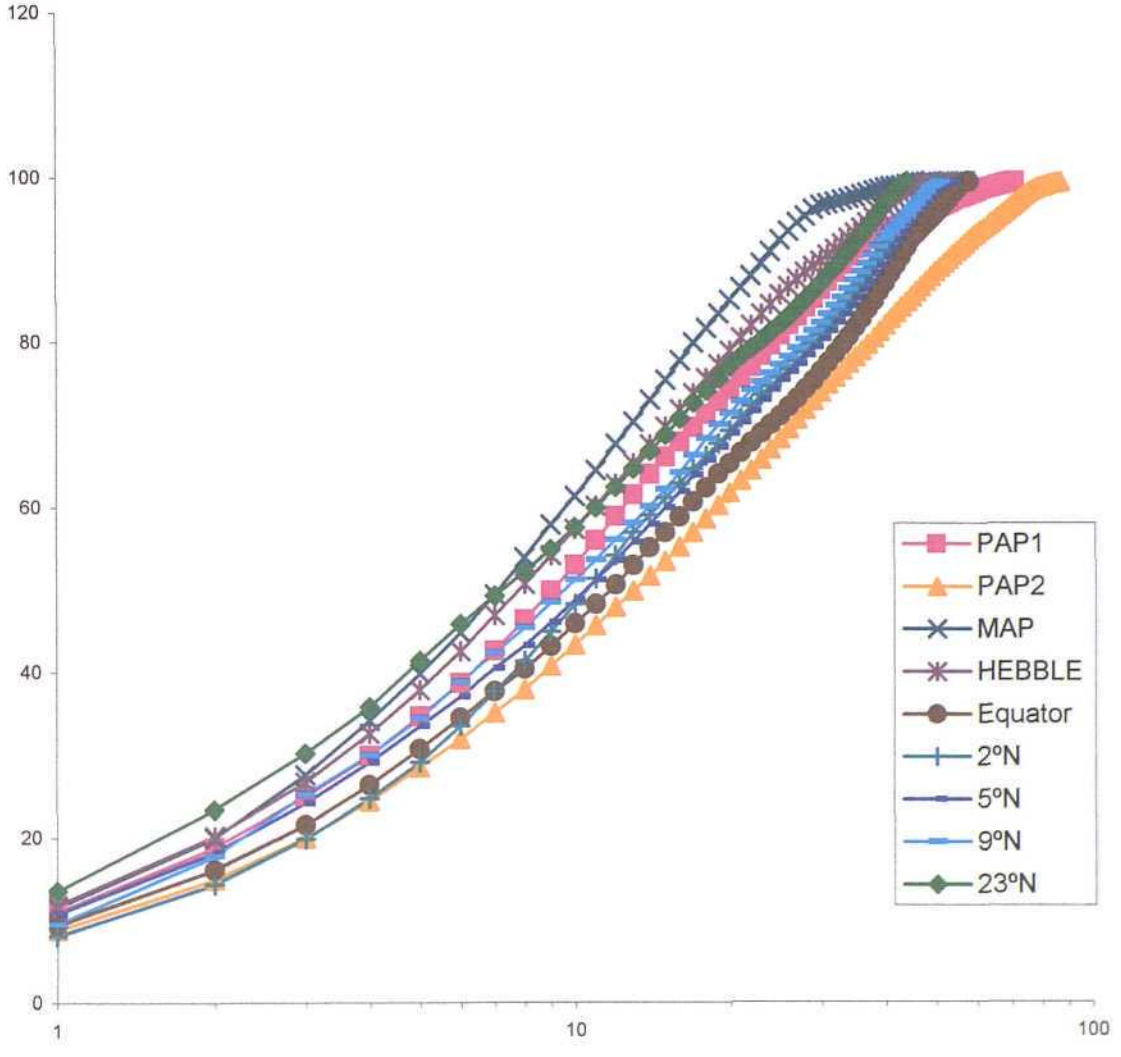
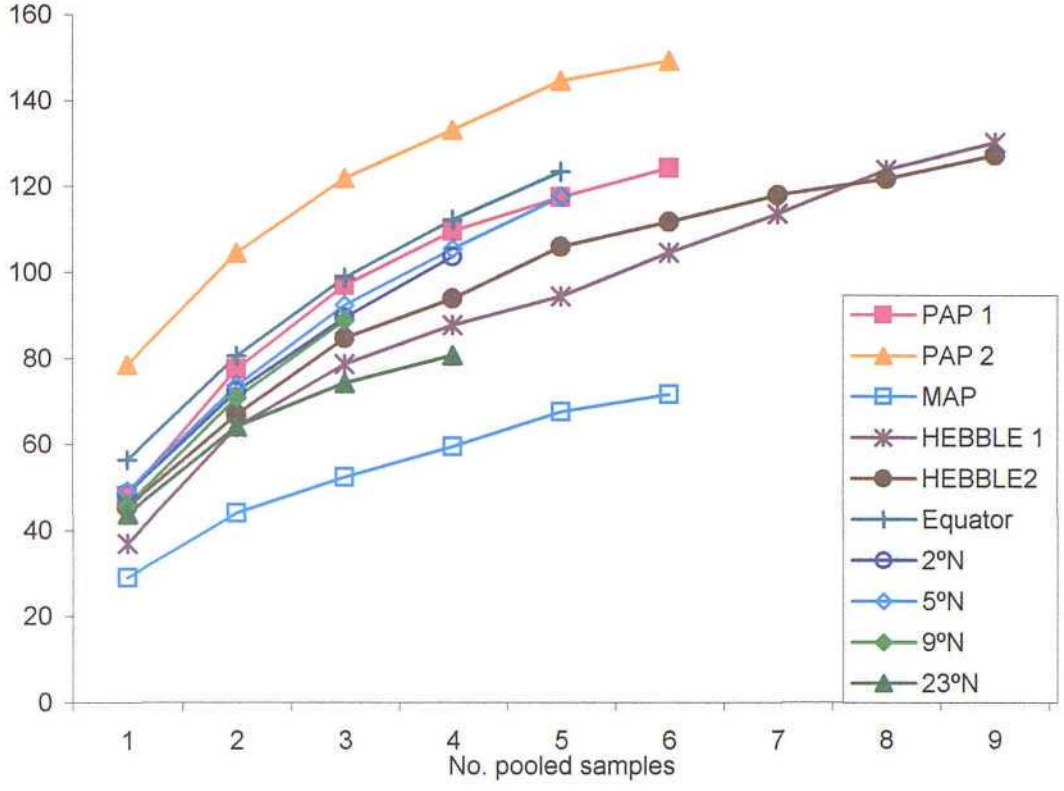


Figure 7.5 Species richness curves for 0-1cm sediment layer at all Pacific and Atlantic stations. See figure 7.2. for explanation of abbreviations used in legend.



Warwick *et al.*, 1990b). It was not possible to use the HEBBLE data as a number of morphological species in the data set had not been assigned to a genus.

After clustering (untransformed data) there was a clear division into Pacific and Atlantic data at 38.7% similarity (Figure 7.6). Within these two clusters there was a general division into stations. The poor clustering within the EqPac dataset compared with that displayed in Chapter 6 (section 6.2.1.4) is due to the comparison of genus-level datasets rather than species lists. This clustering was improved after double-root (√√) -transformation (Figure 7.7). Division into different ocean basins occurred at 44.6% similarity. At 50.7% similarity the Atlantic data was divided into two clusters with PAP2 in one cluster and PAP1 and MAP in the second. This second cluster was divided into the respective stations at 60% similarity with the exception of one PAP1 sample that fell in the MAP cluster.

7.3.4 Comparison of Feeding and Tail-shape Functional Groups

As in chapter 5, each feeding and tail-shape group was treated as an operational classificatory unit (OCU) and the resulting OCU lists for the Atlantic data were combined with the Pacific data. Hierarchical cluster analysis based on the Bray-Curtis index of similarity was then used to assess the functional group composition of all data sets. The HEBBLE data was included in this analysis. The data from PAP2 was not included as no feeding or tail-shape groups had been assigned to the species lists.

The cluster analysis indicated (Figure 7.8) that the samples divided into the two ocean basins at 56.5% similarity, with the exception of a single HEBBLE sample that may be an outlier. The Atlantic basin data divided into NE Atlantic and NW Atlantic samples at 61% similarity and MAP divided from PAP1 at 68% similarity although there was one PAP1 sample included in the MAP cluster. Double-root (√√) -transformation did not improve the clustering and the first division into different ocean basins at 74.7% similarity (Figure 7.9).

An area plot was constructed for the percentage of individuals in each OCU for each sample (as in Chapter 5, section 5.2.3), for stations at HEBBLE, MAP, PAP1 and the EqPac stations (Figure 7.10). Three zones were seen on the area plot that corresponded to

Figure 7.6 Cluster analysis for genera lists for 0-1cm sediment layer at all Pacific and Atlantic stations based upon the Bray-Curtis similarity index (single link Pacific samples have been labelled as in previous chapters. PAP 1-6 = replicates from PAP1, PAP 7-12 = replicates from PAP2 and MAP 1-6 = replicates from MAP. See figure 7.2. for explanation of these station abbreviations.

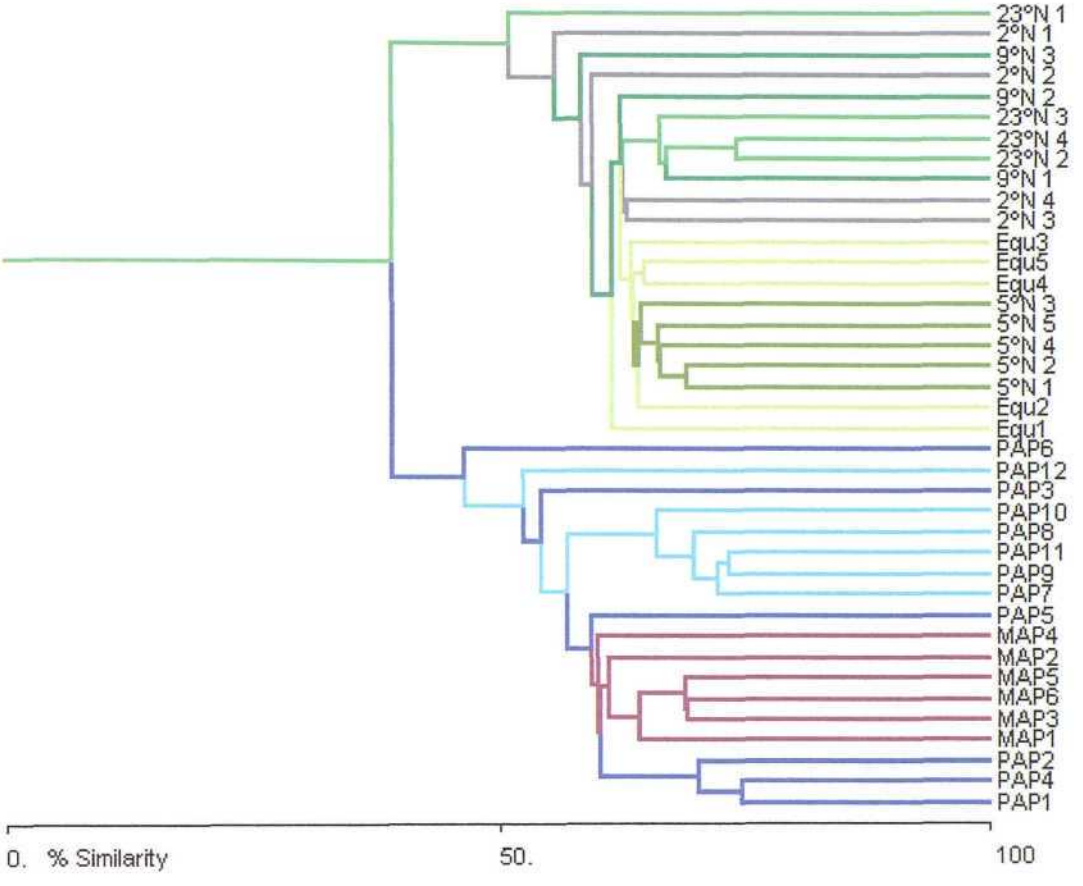


Figure 7.7 Cluster analysis for double-root (√√) -transformed genera lists for 0-1cm sediment layer at all Pacific and Atlantic stations based upon the Bray-Curtis similarity index (single link). Pacific samples have been labelled as in previous chapters. PAP 1-6 = replicates from PAP1, PAP 7-12 = replicates from PAP2 and MAP 1-6 = replicates from MAP. See figure 7.2. for explanation of these station abbreviations.

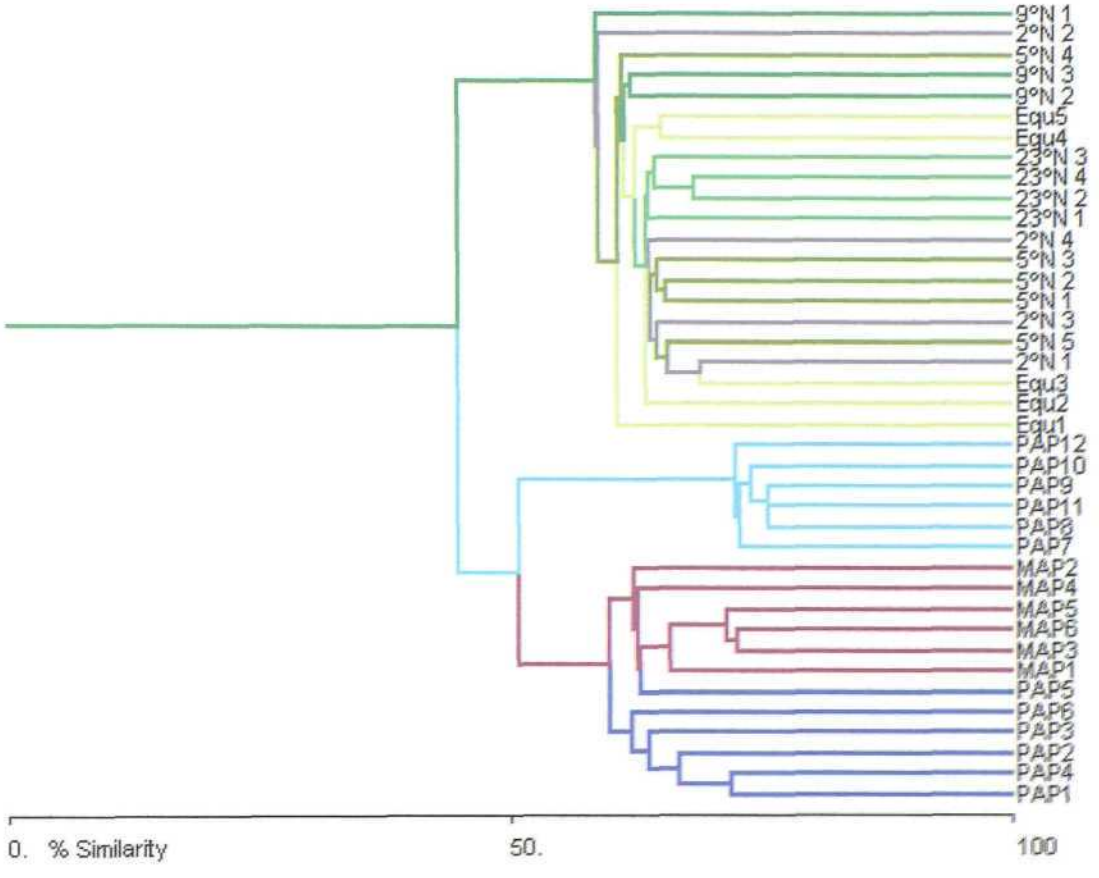


Figure 7.8 Cluster analysis for combined two-way functional groups for 0-1cm sediment layer at all Pacific and Atlantic stations, based upon the Bray-Curtis similarity index (single link). Pacific stations are labelled as in previous chapters. P = PAP, M = MAP, H = HEBBLE and the number refers to replicate number. See figure 7.2. for explanation of these station abbreviations.

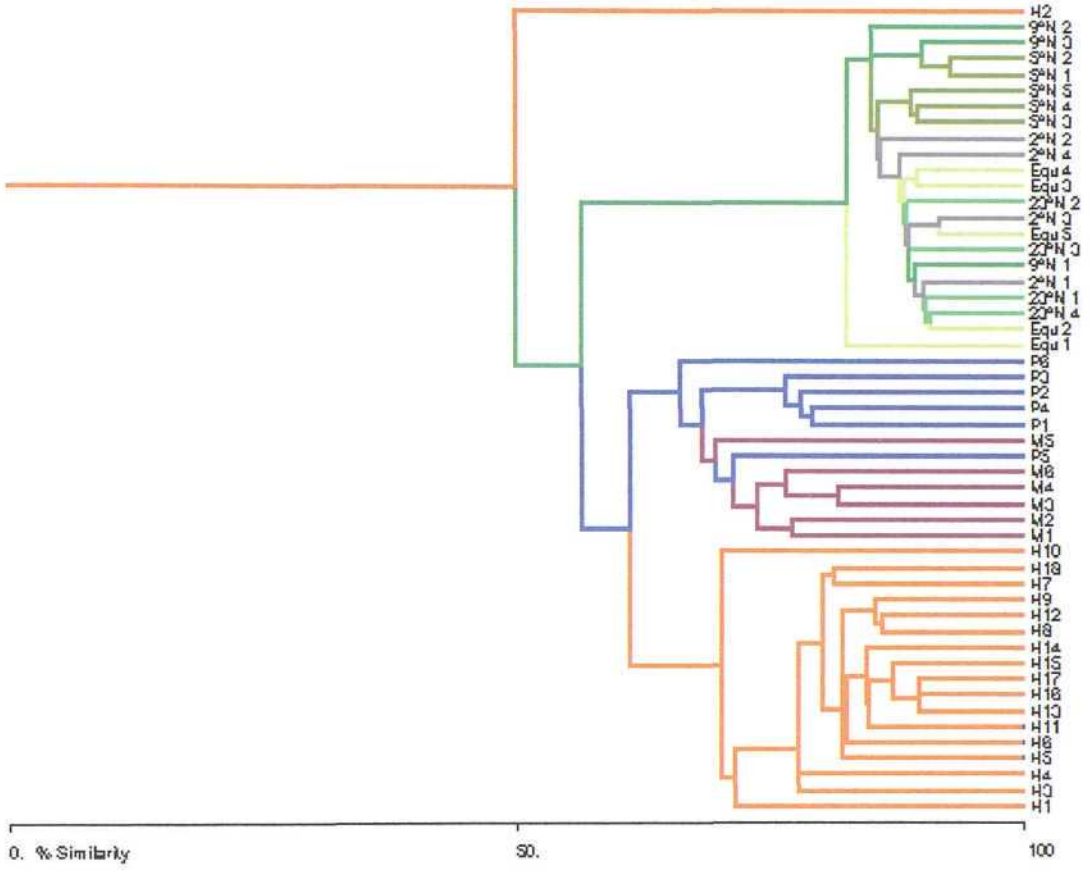


Figure 7.9 Cluster analysis for double-root (√√)-transformed, combined two-way functional groups for 0-1cm sediment layer at all Pacific and Atlantic stations based upon the Bray-Curtis similarity index (single link). Pacific stations are labelled as in previous chapters. P = PAP, M = MAP, H = HEBBLE and the number refers to replicate number. See figure 7.2. for explanation of these station abbreviations.

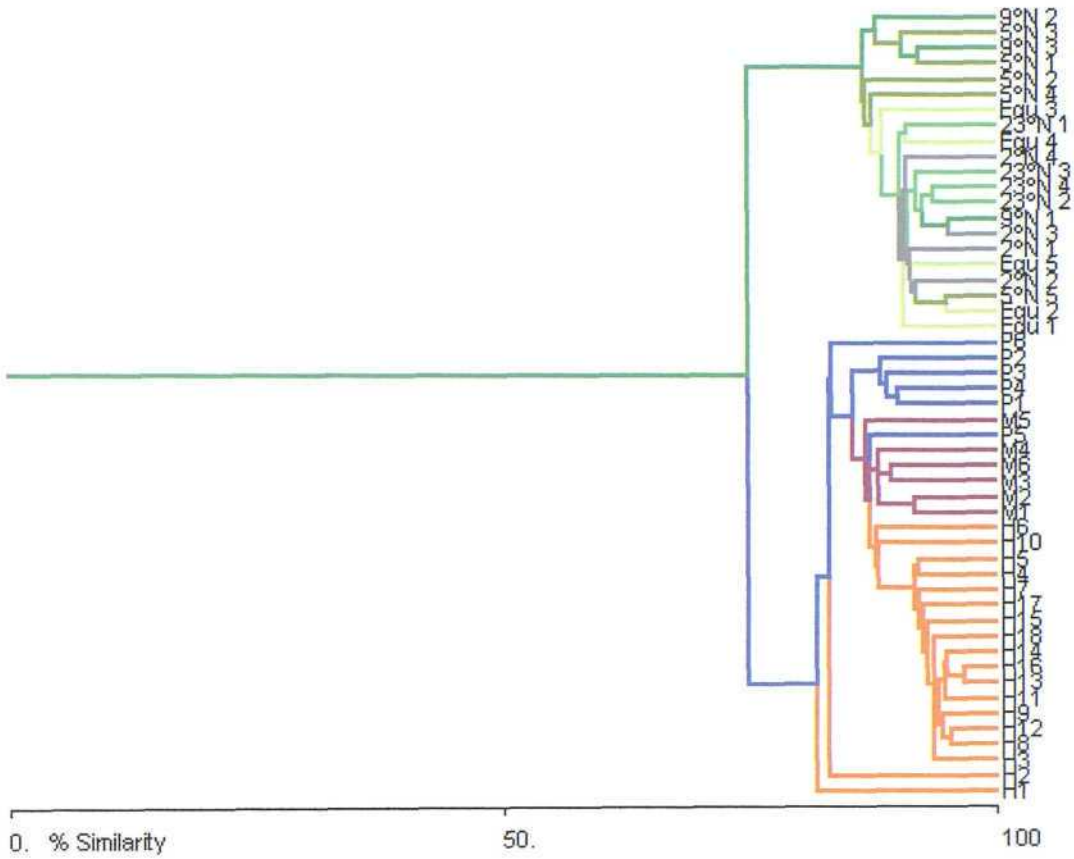
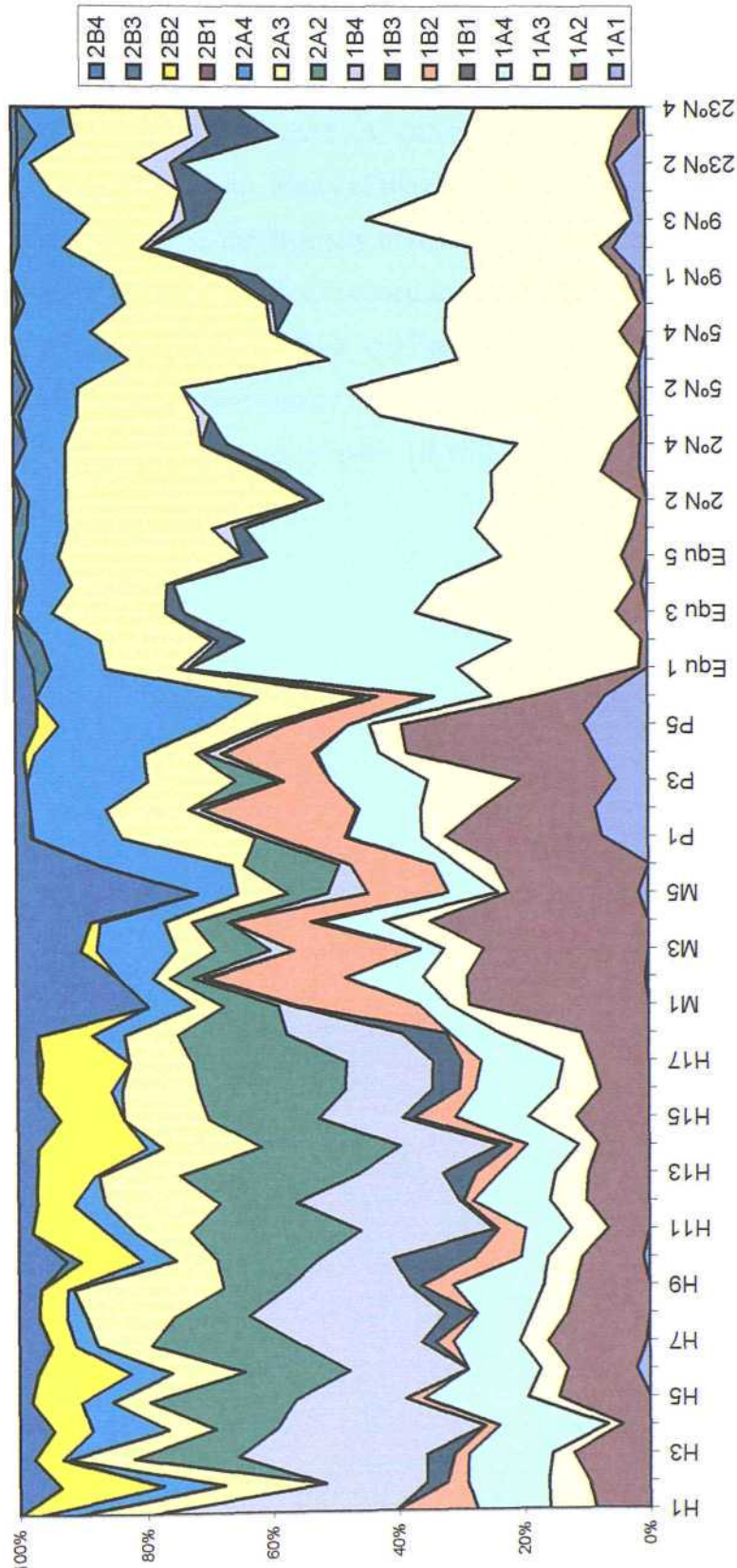


Figure 7.10 Area plot of combined two-way functional groups as percentage of individuals per sample, for the surface (0-1cm) sediment layer for all Pacific and Atlantic stations. PAP 1-6 = replicates from PAP1, MAP 1-6 = replicates from MAP and H 1-18 = replicates from HEBBLE. See figure 7.2. for an explanation of these station abbreviations.



major geographic area. The first zone corresponded to the HEBBLE samples, the second included samples form MAP and PAP1, and the third zone contained all of the EqPac samples. There appeared to be little division within the second and third zones into stations.

At HEBBLE, there was quite an even distribution of individuals between each OCU. This was in contrast to the EqPac stations, which showed dominance by three groups, 1A with conical tails, 1A with filamentous tails and 2A with conical tails. A fourth group, 2A with filamentous tails, was sub-dominant. Many of the other OCU groups were lost almost completely, suggesting a drop in the diversity of morphological types in the equatorial Pacific. The samples from MAP and PAP seemed to be intermediate in terms of dominance and diversity between HEBBLE and EqPac samples. All of the groups that were present at HEBBLE were represented but there was some dominance by three groups, 1A with clavate-conicocylindrical tails, 1B with clavate-conicocylindrical tails and 2A with filamentous tails.

7.4 Discussion

When the North Atlantic stations were compared, PAP, which does receive an input of phytodetritus had higher local diversity (as measured by H' and rarefaction) than either MAP or HEBBLE although, interestingly, evenness was similar to HEBBLE, but significantly lower than MAP. Estimates of local diversity at each station, examined in both ocean basins, indicated that Shannon H' diversity and rarefaction diversity are both high in areas that are known to receive an input of phytodetritus. Along the EqPac transect, nematode communities at stations from 0-5°N have similar H' diversity as at PAP in the NE Atlantic. In addition, H' and rarefaction diversity estimates for nematode assemblages at 9 and 23°N in the Pacific were similar to estimates for stations in the North Atlantic that do not receive an input of phytodetritus. This is in contrast to the effects of phytodetritus on foraminiferal assemblages where diversity either remains unchanged or is actually depressed (Gooday and Lambshead, 1989; Gooday, 1990; Lambshead and Gooday, 1990).

The present study is the first to report a correlation between phytodetritus and local diversity of nematode assemblages. The positive effects on nematode diversity are in contrast to studies of macrofauna (Paterson *et al.*, 1998), where there were no observed changes in species richness, diversity or equitability that could be correlated with increased productivity of the surface waters. Generally, organic enrichment is considered to suppress diversity and evenness (e.g. review in Pearson and Rosenberg, 1978), but this is a typical community response following substantial organic loading. The present study is in agreement with the predictions of Grassle and Morse-Porteous' (Grassle and Morse-Porteous, 1987) Spatio-temporal Mosaic Theory, which suggested that phytodetritus acting as a low-level enrichment effect would increase environmental heterogeneity and consequently enhance local diversity.

The reason for the low evenness but high H' diversity recorded from PAP1 and PAP2, compared with MAP and the EqPac stations, is unclear. In a study of intertidal nematodes in Strangford Lough, N Ireland, Lambshead and Platt (1988) noted that a catastrophic collapse in nematode assemblages was recorded as a sharp drop in diversity (H') and equitability. This was followed by a rapid increase in equitability, whereas H' diversity

was slower to recover. It has been suggested that the nematode assemblages at MAP are still recovering from the effects of a turbidity current that buried the sampling area under turbidite sediments several thousand years ago (Lambshead *pers. comm.*). It is possible that this is the reason for the elevated evenness at MAP that is not mirrored in Shannon H' diversity. Whilst the HEBBLE site is also characterised by turbidite sediments, the nematode assemblages are disturbed regularly on an intra-annual timescale by benthic storm events (Hollister and Nowell, 1991).

In chapter 6 (section 6.2.1), the nematode communities of the abyssal equatorial Pacific were shown to be strongly dominated by species belonging, in order, to the Monhysteridae, Chromadoridae, Microlaimidae and Xyalidae. Closer examination of the species lists for PAP and MAP found that the samples were dominated by the same families (Table 7.5). All NE Atlantic samples were dominated by the Chromadoridae and at PAP2, the next most dominant families were the Monhysteridae and the Xyalidae. At PAP1 and MAP, the Chromadoridae were followed by the Xyalidae and then the Monhysteridae, although the latter were less well represented at MAP. This suggests that, at the family level, there is a characteristic response by particular groups of nematodes to phytodetritus. In the equatorial Pacific, it was hypothesised that the monhysterids, which are thought to be primarily bactiverous, responded opportunistically to phytodetritus. Similarly, the Xyalidae occurred in greatest abundance at stations at 9 and 23°N where no phytodetritus has been observed. This is in agreement with greater abundance of this family at MAP compared with PAP2.

It is possible that differences in the nematode assemblages at PAP1, compared with those at PAP2, have arisen due to seasonal changes in the communities. PAP2 was sampled during August-September whereas PAP1 was sampled during May. Phytodetritus deposition has been observed to arrive at the seafloor during May-June each year at PAP (Rice *et al.*, 1986), and in accordance with the five-month response time proposed in chapter 4 (section 4.3), PAP nematode assemblages would not have had time to respond to the phytodetrital event before the PAP1 sampling programme occurred. Alternatively, there may be some taxonomic bias. PAP1 samples were identified by a different researcher at the Natural History Museum than samples from PAP2. No measure of the degree of potential bias has been made at the current time.

Table 7.5 Dominant (>10%) and subdominant (>5%) families present in 0-1cm sediment layer from MAP and PAP in the NE Atlantic.

PAP1			PAP2			MAP		
	Mean	%		Mean	%		Mean	%
CHROMADORIDA	52.33	26.32	CHROMADORIDAE	48.33	21.37	CHROMADORIDA	27.67	29.33
XYALIDAE	36.50	18.36	MONHYSTERIDAE	43.00	19.01	XYALIDAE	22.33	23.67
MONHYSTERIDAE	33.33	16.76	XYALIDAE	41.83	18.50	MONHYSTERIDAE	11.00	11.66
OXYSTOMINIDAE	20.33	10.23	DESMOSCOLECID	22.17	9.80	OXYSTOMINIDAE	10.83	11.48
DIPLOPELTIDAE	11.67	5.87	OXYSTOMINIDAE	17.00	7.52	CYATHOLAIMIDA	5.00	5.30
			DIPLOPELTIDAE	14.33	6.34			

At the genus level, the Pacific samples were dominated by *Thalassomonhystera*, *Acantholaimus* and *Halalaimus* in that order. PAP2 was also dominated by species belonging to the *Thalassomonhystera* genus, followed by *Acantholaimus* and *Halalaimus* species (Table 7.6). At PAP1, *Thalassomonhystera* was superseded by *Acantholaimus* and at MAP, the numbers of individuals belonging to the *Thalassomonhystera* genus was considerably reduced. Gooday (1990) noted the occurrence of a foraminiferan that preferentially colonised phytodetritus, and the occurrence of high numbers of a particular *Thalassomonhystera* species within phytodetrital aggregates at the BIOTRANS site in the NE Atlantic (Thiel *et al.*, 1988/89) has already been discussed in chapter 6. This seems to reinforce the proposal that there is a characteristic nematode phytodetrital fauna, regardless of ocean basin.

Although the dominant genera at each site receiving phytodetritus bear many similarities, this is not reflected in the Bray-Curtis cluster analysis. Rather than forming clusters for stations that do receive phytodetritus, and stations that do not, the clusters are separated by location. Clustering is reinforced by transforming the data, which reduces the weighting by dominant species. This suggests that it is the rarer species at each station that are responsible for the differences in community structure at each location. It is likely that these differences represent a biogeographic effect rather than a phytodetrital response.

Regional diversity is also correlated with an input of phytodetritus and elevated POC fluxes. Collectors curves indicate that species richness is greater for all stations receiving phytodetritus, regardless of location, than those stations that do not. As different taxonomists compiled the species lists for the two oceans, it is impossible to prove conspecificity without considerable additional work. Consequently, it is also impossible to perform a regression analysis on local diversity *vs.* regional diversity as advocated by Stuart and Rex (1994) and Rex *et al.* (1997), to examine the relationship between local and regional diversity in this instance. Based upon the work of these authors, which demonstrated that local and regional diversities were highly inter-dependent, it is proposed that phytodetritus does increase local diversity by enhancing the regional species pool.

Unfortunately, the regional enrichment model does not adequately explain the high local diversity exhibited by nematodes and harpacticoid copepods. Rex *et al.* (1997)

Table 7.6 Dominant (>5%) and sub-dominant (>1%) genera present in the 0-1cm sediment layer from MAP and PAP in the NE Atlantic

PAP1			PAP2			MAP		
	Mean	%		Mean	%		Mean	%
Acantholaimus	30.17	15.17	*Thalassomonhystera*	39.17	17.32	*Acantholaimus*	22.67	24.03
Thalassomonhystera	29.83	15.00	*Acantholaimus*	27.17	12.01	*Thalassomonhystera*	11.00	11.66
Halalaimus	17.83	8.97	*Halalaimus*	15.83	7.00	*Daptonema*	10.83	11.48
Elzalia	12.67	6.37	*Prochromadorella*	14.50	6.41	*Halalaimus*	10.50	11.13
Chromadorina	9.83	4.95	*Enchonema*	14.33	6.34	*Xyalidae*	4.17	4.42
Quadricoma	9.33	4.69	*Daptonema*	11.83	5.23	*Metadesmolaimus*	3.33	3.53
Daptonema	8.83	4.44	*Pareudesmoscolex*	9.67	4.27	*Campylaimus*	3.33	3.53
Campylaimus	8.17	4.11	*Desmoscolex*	8.83	3.91	*Cyatholaimid*	2.83	3.00
Microlaimus	7.67	3.86	*Molgolaimus*	8.50	3.76	*Amphimonhystrella*	2.83	3.00
Desmoscolex	5.33	2.68	*Campylaimus*	8.50	3.76	*Pompenema*	1.50	1.59
Actinonema	4.00	2.01	*Quadricoma*	6.83	3.02	*Quadricoma*	1.50	1.59
Aegialoalaimus	3.83	1.93	*Elzalia*	5.83	2.58	*Chromadora*	1.33	1.41
Xyalidae	3.50	1.76	*Diplopeltula/toides*	5.83	2.58	*Cyartonema*	1.33	1.41
Prochromadora	3.17	1.59	*Diplolaimella/oides*	3.83	1.69	*Desmoscolex*	1.33	1.41
Linhystera	3.17	1.59	*aff.Pareudesmoscolex*	3.67	1.62	*Actinonema*	1.17	1.24
Metadesmolaimus	3.00	1.51	*Manganonema*	3.67	1.62	*Innocuonema*	1.17	1.24
Diplopeltula	2.83	1.42	*aff Karkinochromador*	3.00	1.33	*Dolicholaimus*	1.00	1.06
Sceptrella	2.67	1.34	*Aegialoalaimus*	2.50	1.11	*Syringolaimus*	1.00	1.06
Pierrickia	2.50	1.26	*Amphimonhystrella*	2.50	1.11	*Diplopetoides*	1.00	1.06
Amphimonhystrella	2.17	1.09						
Monhysterida	2.00	1.01						

hypothesised that species with planktotrophic development and, consequently, fast dispersal, should have the highest local diversity. Nematodes, however, are viviparous and lack a larval dispersal phase. Furthermore, the quiescent conditions of the deep sea offer limited opportunities for passive dispersal. In this instance, it is more likely that local diversity is driving regional diversity.

The functional groups of the EqPac nematodes seem to suggest that morphological diversity is reduced in the central Pacific compared with the NW and NE Atlantic samples. The Pacific samples are very distinct compared with Atlantic samples and there was no apparent transition that marked stations that do receive phytodetritus from those that do not. Similarly, in the Atlantic samples, PAP assemblages bore greater resemblance to MAP and HEBBLE assemblages, than they do to the Pacific stations that receive phytodetritus. This was unexpected, given the taxonomic similarities at the genus level described above.

In the central Pacific, nematode communities were dominated by predominately four functional groups, 1A3 (selective deposit feeders with a conical tail), 1A4 (selective deposit feeders with filamentous tails), 2A3 (epistrate feeders with a conical tail) and 2A4 (epistrate feeders with a filamentous tail), whereas the Atlantic samples have a number of other groups that are dominant. The functional group composition of the Pacific assemblages directly contradicts competition theories which argue that organisms will become increasingly specialised in order to avoid competitive exclusion (Sanders, 1968).

It is possible that the reduced functional groups do not adequately represent functional guilds and present an over-simplified picture where much of the information has been lost. This certainly appears to be the case in the Atlantic where more functional groups are represented. Because of the regional nature of the functional group distributions, it is more likely that an evolutionary response is responsible for the patterns observed than an ecological one.

At the end of the Cretaceous period of geological history, the deep global ocean experienced a rapid (on evolutionary time-scales) increase in temperature of 15°C, followed by a decrease in temperature and an increase in seasonality during the Early

Cenozoic (Cox and Moore, 1993). This increase in temperature resulted in an increase in oxygen tension (Roth, 1989), that may have been catastrophic to nematodes belonging to particular functional groups. Whilst nematodes are known, in general, to be tolerant of hypoxic conditions (Giere, 1993), community analysis of assemblages inhabiting the sediments of a Swedish fjord following a hypoxia event noted that functional group and species diversity were drastically reduced (Austen and Wibdom, 1991; Hendelberg and Jensen, 1993). Subsequent species radiation in the deep sea, following a return to lower temperatures and lower oxygen tension, would then have been restricted to those morphological types remaining.

Approximately sixty million years ago, the abyssal Atlantic had not yet been formed (Press and Siever, 1986). As the Atlantic formed by seafloor-spreading at the Mid-Atlantic Ridge, colonisation of abyssal sediments may have occurred from the adjacent continental shelf and slope. Colonisation of deep-sea sediments from sublittoral ecosystems has been proposed for other groups of fauna, including amphipods (Just, 1980) and janiroidean and flabelliferan isopods (Hessler and Wilson, 1983; Wilson, 1998). PAP, MAP and HEBBLE are all located close to the foot of the continental rise so migration of nematodes down-slope is likely, whereas the Pacific samples were collected a greater distance from the North American continental shelf. In addition, analysis of the functional group composition of sublittoral and slope assemblages indicates similarities that suggest invasion of the North Atlantic abyssal sediments in this manner is plausible (Collins, *unpublished*). From this it can be postulated that evolutionary events rather than ecological events are responsible for the functional group composition of central Pacific nematode assemblages.

7.5 Conclusions

- Phytodetritus and elevated POC fluxes are correlated with an increase in nematode regional diversity. However, in contrast to hypotheses by a number of workers (Ricklefs, 1987; Grassle and Maciolek, 1992; Ricklefs and Schluter, 1993; Rex *et al.*, 1997), it is more likely that local-scale processes drive regional diversity in deep-sea nematode assemblages due to the absence of a dispersal stage in nematode life histories.

- At the genus level, there is a characteristic nematode assemblage common to sediments receiving an input of phytodetritus that occurs both in the equatorial Pacific and the NE Atlantic.

- Functional group composition cannot be adequately explained by ecological events as diversity can, and instead may possibly be controlled by historic events that occurred on an evolutionary time-scale.

8.1 General Summary

There were two main aims to the present study; the first was to make a detailed analysis of the effects of phytodetritus on nematode communities of the equatorial Pacific, and the second was to compare these results with those from other phytodetrital-receiving areas in the NE Atlantic. This study comprises the first detailed taxonomic assessment of nematode communities in the abyssal Pacific, in addition to constituting part of the multi-disciplinary, equatorial Pacific process study.

Increased POC flux was positively correlated with an increase in nematode abundance and total biomass along the JGOFS EqPac transect. Nematode biomass was highly correlated with POC flux measured into sediment traps 2000m above the seabed (Honjo *et al.*, 1995), but the correlation between abundance and POC flux was less marked. The results appear to suggest that the *K*-strategy life-history prevails in the abyssal nematodes of the equatorial Pacific, i.e. the nematodes are eating to increase body size rather than for reproductive output. This contradicts the dominance by characteristically opportunistic species such as *Thalassomonhystera sp.* This may be explained in terms of the high evenness also seen at the EqPac stations that do receive phytodetritus, i.e. the opportunistic species account for a small proportion of the total community. Using time-averaged POC flux measured into deep-moored sediment traps, the current study also indicated that abyssal nematode communities in the equatorial Pacific may respond to enhanced POC flux on a five-month timescale. Previous work that has failed to correlate nematode abundance and biomass with phytodetrital input and POC flux (Pfannkuche, 1992; Gooday *et al.*, 1996) may be explained by the use of response time-scales more appropriate to shallow-water nematodes.

Vertical profiles of abundance and biomass suggested some degree of upwards migration at stations at the equator and 5°N, particularly by larger individuals. There was little evidence of increased abundance of larger organisms influencing the vertical distribution of nematode abundance or biomass, in contrast to previous studies. However, greater intra-station variability in both abundance and biomass in the equatorial and 5°N samples

might be due to bioturbation events, such as surface sediment cropping or mixing down of labile organic carbon. Bioturbation activity (as indicated by radioisotope proxies) and megafaunal standing stocks were significantly higher at these two stations (Smith *et al.*, 1997).

The greater POC flux experienced between 0 and 5°N was also correlated with an increase in the abundance of 1A and 2A feeding types. The 1B feeding type was significantly more abundant at stations at 9 and 23°N. When compared with other abyssal sites where trophic composition has been studied (Tietjen, 1984; Thistle and Sherman, 1985; Rutgers van der Loeff and Lavaleye, 1986; Thistle *et al.*, 1995), it was suggested that 1B may be the typical feeding type in the deep sea and 1As increase in abundance when food availability (implied by increased POC flux and presence of phytodetritus) increases. This suggests a switch to a more catholic diet in areas of reduced food availability, in direct contradiction of competition theories. In addition, the increased abundance of 2As was correlated with the occurrence of phytodetritus. Shallow-water experiments have observed that nematodes belonging to this feeding type feed on diatoms (Jensen, 1983; Romeyn and Bouwman, 1983; Trotter and Webster, 1984; Jensen, 1987) and the occurrence of intact centric and pennate diatoms in equatorial Pacific, phytodetrital aggregates (Smith *et al.*, 1996) suggests that 2A nematodes may have a similar diet.

Within-habitat species diversity was significantly higher at stations from 0-5°N than at stations from 9-23°. This was expressed in terms of Shannon's H', J' and rarefaction diversity. All α diversity measures were significantly correlated with annual POC flux. H' and J' values for samples from 9 and 23°N fell within the range recorded from other deep-sea stations in the North Atlantic where phytodetritus has not been observed. Species diversity in samples from stations at 0-5°N were not significantly different from the diversity of samples collected at PAP in the NE Atlantic that does receive a phytodetrital input.

At the genus level there was a characteristic fauna that was dominant in all samples from stations that receive an input of phytodetritus. The same faunal group was also dominant in samples from the Porcupine Abyssal Plain in the NE Atlantic. This suggests that there is a typical assemblage that can be identified as a "phytodetrital" fauna, at least at the genus

level. Cluster analysis separated the samples on an ocean basin basis, but the clustering was reinforced by double-root transformation indicating that it is the presence of rare genera that are important in determining dissimilarities, a feature characteristic of deep-sea benthic communities. These can not be attributed to phytodetrital effects and it was concluded that it is possible that the distinct communities identified in the cluster analysis arise as a consequence of biogeographical effects, rather than a phytodetrital response.

Similarly, regional species richness in the equatorial Pacific was also correlated with annual POC flux. When Pacific and North Atlantic Ocean samples were combined, there was a clear pattern for increased regional diversity in areas that have reported to receive an input of phytodetritus. It was concluded that increased POC flux increases local nematode diversity, which, in turn, maintains high regional diversity in contrast to the studies of Ricklefs (1987), Stuart and Rex (1994) and Rex *et al* (1997).

The equatorial Pacific data set also offers a unique opportunity to test theories of the causes of latitudinal gradients. On a biogeographical scale, it is generally accepted in terrestrial systems that species diversity decreases with increasing latitude. Coastal marine and open-ocean pelagic ecosystems seem to show a similar pole-ward decline in diversity (Rex *et al.*, 1997). Sanders (1968) originally proposed that deep-sea benthic macrofauna also followed this pattern, although his methodology was flawed and hence his argument controversial. More recently, Rex *et al* (1993) investigated Sander's proposal using standardised techniques for samples collected between 37°S and 77°N in the Atlantic Ocean. In the North Atlantic their results confirmed Sander's (1968) hypothesis, at least for isopods, gastropods and bivalves. All of these groups demonstrated a significant decline in diversity with increasing latitude. These latitudinal gradients were unexpected because it was assumed that the environmental gradients that are responsible for large-scale gradients on the surface, were absent from the deep sea. Rex *et al* (1993) proposed that these latitudinal gradients were influenced by surface production and benthic flux, which both increase towards the poles. Thomas and Gooday (1996) also recorded lower diversity in Cenozoic benthic foraminifera collected from the Southern Ocean compared with lower latitudes. They suggested that the species-richness gradient resulted from an increasing but highly seasonal food influx into the deep ocean just prior to and during formation of the Antarctic ice sheets. Decreased or more variable food supply at high

latitudes was also thought to be responsible for lower Pliocene isopod diversity (Cronin and Raymo, 1997).

Similar latitudinal diversity patterns have not been consistently recorded from shallow sub-littoral studies, however. A study examining macrofauna samples from the Arctic (78°N), a temperate site (55°N) and a tropical site (7°S) in the Atlantic Ocean found similar diversity at all stations (Kendall and Aschan, 1993). Other studies have demonstrated a unimodal, temperate peak (Thorson, 1957) or reversed gradients (Santelices, 1989). Using the same methodology, Dauvin *et al* (1994) also failed to find bathyal latitudinal gradients in polychaetes in the NE Atlantic, as described by Rex *et al* (1993) for other macrofaunal taxa. Boucher and Lambshead (1995) examined a suite of nematode samples, collected from seventeen standardised data sets from six biotopes; temperate estuarine, tropical sublittoral, temperate sublittoral, bathyal, abyssal and hadal. Nematodes were also found to lack any shallow-water, latitudinal diversity gradient - the tropical sublittoral samples had either similar or lower diversity than the temperate sublittoral samples. A study by Lambshead *et al,* (in prep.) suggests that in addition to shallow water sites, latitudinal gradients are also absent in deep-sea nematodes from the NE Atlantic.

These patterns of latitudinal diversity in the deep NE Atlantic are thought to be partially confounded by recovery of the regional species pool from Quaternary glaciation (Rex *et al.*, 1993). For the first time, the samples collected from the equatorial Pacific offer the opportunity to examine gradients of species richness affected only by an ecological variable, with no historic influences. It was clearly demonstrated that phytodetritus acts to enhance species diversity on a regional scale over a broad latitudinal range (23°). This suggests that the declining diversity gradient, that conflicts with increasing surface production and vertical flux in the NE Atlantic, has indeed been influenced by historic events. The effects of glaciation were felt in shallow and deep waters in the Norwegian Sea and as far south as 50°N (McIntyre *et al.*, 1976; Andrews, 1979) and offer the best explanation for the low species diversity recorded from these areas.

To conclude, it is apparent that an increased particulate organic carbon flux has a profound effect on abyssal nematode communities, both in terms of community standing stock (i.e.

abundance and biomass), trophic structure and biodiversity. The present study provides a comprehensive view of abyssal nematode communities and the impact of phytodetritus and POC flux upon them, that is unparalleled at the present time.

8.2 Recommendations

Although a very comprehensive study and well-grounded on a substantial environmental data set provided by other participants in the EqPac process study, there are a number of aspects that could have improved the study.

- At some stations, especially at 9°N, and for the vertical profiles, there was a very low number of replicates used for the study. This purely reflects a time constraint – a further twelve months would be required to work up further samples so that all stations and sediment depths were represented by five, or better six, replicates. Six replicates would have been statistically more robust and would have provided better information regarding intra-station variability.

- The US JGOFS EqPac study represents a single time period, although there is spatial variability. Much more information is required over time, whether sampling is inter-annual, at the same time every year, or intra-annual, to determine temporal variation during the year. It is known that tropical instability waves that intensify the convergence zones (Yoder *et al.*, 1994), occur more frequently during autumn and, in turn, affect the vertical POC flux in the area (Honjo *et al.*, 1995). This would be expected to have an effect on the nematode communities, particularly their standing stock.

- Currently, no information exists regarding the diet of deep-sea nematodes. The equatorial Pacific potentially offers the opportunity to observe trophic organisation and particle selection using radionuclides. ^{234}Th is naturally scavenged by particles that are sinking through the water column. Material that is recently arrived at the abyssal seafloor consequently emits excess activity that is easily recorded, even from preserved material (Stephens *et al.*, 1997). It has been postulated in the present study that deposit feeders in the abyssal equatorial Pacific are feeding on bacteria colonising the phytodetrital material. It may be possible, using radionuclide tracers, to test whether this food source of the postulated deposit-feeders can be established.

Station: Equator
Surface 0-1cm

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC4 V6	BC6 V14	BC7 V15	BC8 V16	MC15 Tube2
ENOPLIDA	ENOPLIDAE	Trichenoplus	sp.A	2B	3					1
	THORACOSTOMOPSIDAE	Paramesacanthion	sp.A	2B	3		2			
	PHANODERMATIDAE	Phanodermatidae	sp.A	1A	3	1				
		Phanodermatidae	sp.B	1A	4	1				
	IRONIDAE	Syringolaimus	sp.A	2A	3		1			1
		Syringolaimus	sp.B	2A	3		1			
	OXYSTOMINIDAE	Halalaimus	sp.A	1A	4			2	1	1
		Halalaimus	sp.B	1A	4		1			
		Halalaimus	sp.C	1A	4		3			
		Halalaimus	sp.D	1A	4	2	1	1	1	1
		Halalaimus	sp.E	1A	4					1
		Litinium	sp.A	1A	1				1	
		Litinium	sp.B	1A	3	1				
		Oxystomina	sp.A	1A	2					1
		Oxystomina	sp.B	1A	2					1
		Oxystomina?		1A	2		1			
		Thalassolaimus	sp.A	1B	3		1			
	ONCHOLAIMIDAE	Adoncholaimus?		2B	2			1		
		Viscosia?		2B	3	2				
		Metoncholaimus?		2B	3				1	
		Metaparaoncholaimus?		2B	4	1				
		Oncholaimidae indet		2B	3		1			
	ENCHELIDIIDAE	Bathyeurystomina	sp.A	2B	4	1	1			
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp. indet	2A	4		2		1	1
		Acantholaimus	sp. A	2A	4	3	3	3	2	2
		Acantholaimus	sp. B	2A	4	2	3	2	4	2
		Acantholaimus	sp. C	2A	3	1	1			2
		Acantholaimus	sp.D	2A	4	1				
		Actinonema	sp.A	2A	3	1	2		4	5

	Endeolophos	sp.A	2A	3					1
	Prochromadorella	sp.A	2A	3		1			
COMESOMATIDAE	Cervonema?		1A	3	1	2			
CYATHOLAIMIDAE	Cyatholaimidae	sp.A	2A	3		1	1		
	Marylynnia	sp.A	2A	4		1			
	Marylynnia	sp.B	2A	4					1
	Paracanthonchus?		2A	3				1	
DESMODORIDAE	Desmodora	sp.A	2A	3	1	1		2	1
	Desmodora	sp.B	2A	3				1	1
	Desmodora	sp.C	2A	3		3	1		
	Desmodora	sp.D	2A	3		1		1	1
	Paradesmodora	sp.B	2A	3				1	
	Paradesmodora?		2A	3					2
DRACONEMATIDAE	Eudraconema	sp.A	2A	3		1	1		
MICROLAIMIDAE	Aponema	sp.A	2A	3	1	1	3	1	2
	Microlaimidae	sp.B	2A	3					1
	Microlaimidae	sp.C	2A	3					
	Microlaimus	sp.A	2A	3			5	1	2
	Microlaimus	sp.B	2A	3	3	1	3	1	6
	Molgolaimus	sp.A	2A	3			1		1
	Molgolaimus	sp.B	2A	3		1	1		
	Molgolaimus	sp.D	2A	3				1	
	Nox	sp.A	2A	3		1			
	Paramicrolaimus?		2A	3					1
LEPTOLAIMIDAE	Antomicron	sp.A	1A	3	1				
	Camacolaimus	sp.A	2A	3	1		2	1	1
	Camacolaimus	sp.B	2A	3					1
	Dennis gen nov	sp.A	1A	3				1	
	Leptolaimus	sp.A	1A	3		2		2	
	Leptolaimus	sp.B	1A	3	1		8	2	1
	Leptolaimus	sp.C	1A	3	1	1	2		
	Leptolaimus	sp.E	1A	3		1			
	Leptolaimus	sp.F	1A	3			1		
	Leptolaimus/Stephanolaimus		1A	3	1				
	Leptolaimidae?		1A	3			1		

	AEGIALOALAIMIDAE	Cyartonema?		1A	2			1	1	
		Cyartonema	sp.A	1A	2			1		
		Diplopeltiodes	sp.A	1A	3		2	1	1	1
		Diplopeltoides	sp.B	1A	3		3	3	5	4
		Diplopeltoides	sp.C	1A	3				1	1
		Southernia	sp.A	1B	3		1	1		
	TUBOLAIMOIDIDAE	Chitwoodia	sp.A	1A	3				1	
		Tubolaimoides	sp.A	1A	3		1	2		1
	CERAMONEMATIDAE	Pselionema	sp.A	1A	3			1	1	
		Pselionema	sp.B	1A	3		1			
	MEYLIIDAE	Quadricoma	sp.A	1A	3		2	2	3	
		Quadricoma	sp.B	1A	3	1			2	
		Quadricoma	sp.C	1A	3	3	1	3	3	1
		Tricoma/Quadricoma?		1A	3	1	1			2
	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	1	1		1	1
		Desmoscolex	sp.B	1A	3		1	1	1	
		Desmoscolex	sp.C	1A	3	2				
		Desmoscolex?		1A	3	1			1	1
		Desmoscolecidae	sp.A	1A	3	2				
		Amphidless gen nov	sp.A	1A	3			2	1	
MONHYSTERIDA	MONHYSTERIDAE	Geomonhystera?		1A	4					1
		Monhysteridae?		1A	4	2	2	2	2	1
		Monhysteridae	sp.A	1A	4	1	1	5	9	2
		Monhysteridae	sp.B	1A	4	1	2		1	3
		Monhysteridae	sp.C	1A	4	4	5	4	1	6
		Monhysteridae	sp.D	1A	4	1	7	1	1	1
		Monhysteridae	sp.E	1A	4				1	1
		Thalassomonhystera	sp.?	1A	4				1	
		Thalassomonhystera	sp.A	1A	4	2	5	7	8	9
		Thalassomonhystera	sp.B	1A	4	10	6	8	5	5
		Thalassomonhystera	sp.C	1A	4		1		1	1
		Thalassomonhystera	sp.D	1A	4	2	4	1	2	2
		Thalassomonhystera	sp.E	1A	4	1	1			
		Thalassomonhystera	sp.F	1A	4		1			
	XYALIDAE	Amphimonhystera	sp.A	1A	4				1	

	Amphimonhystera	sp.B	1A	4					1	
	Cobbia?		1A	4					1	
	Desmolaimus?		1B	3						1
	Linhystera	sp.A	1A	4	1		1		1	
	Manganonema	sp.A	1A	4	2	1	5		3	2
	Metadesmolaimus?		1B	3					1	
	Xyalidae?		1B	3		1	1			
	Xyalidae	sp.A	1A	4					1	
	Xyalidae	sp.B	1A	3						1
	Xyalidae	sp.C	1A	3		1				1
	Xyalidae	sp.D	1A	3					1	
	Xyalidae	sp.E	1B	4	1	1				
LINHOMOEIDAE	Linhomoeidae?		1B	3						1
	Paralinhomoeus?		1B	3		1				1
SPHAEROLAIMIDAE	Metasphaerolaimus	sp.A	2B	1					1	
AXONOLAIMIDAE	Ascolaimus?		1A	3			1			1
DIPLOPELTIDIDAE	Campylaimus	sp.A	1A	2			1			2
	Campylaimus	sp.B	1A	2	1		2			
	Diplopeltula	spA	1A	3	1					
	Diplopeltula	sp.B	1A	3			3		1	2
	Diplopeltua	sp.C	1A	3			1		3	1
	Pararaeolaimus	sp. A	1A	3	1					
	Southerniella	sp.A	1B	3			1			1
	Indet 2			3						1
	Indet 3		2A	3	1					
	Indet 6		1A	4	1					
	Unkn		1A	3	2	1	1			
	unkn3							1		
	unkn chromadorid?								1	

Station: 2°N
Surface 0-1cm

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC9 V12	BC10 V17	BC11 V12	BC12 V17
ENOPLIDA	THORACOSTOMOPSIDAE	Paramesacanthion/Mesacanthion		2B	4				1
	ANOPLOSOMATIDAE	Anoplostoma	sp.A	1B	4	1			
	PHANODERMATIDAE	Phanodermopsis?		1A	3			1	
		Micoletzkyia?		1A	3		1		
		Phanodermatidae	sp.A	1A	3			1	
		Phanodermatidae indet.		1A	2			1	2
	IRONIDAE	Syringolaimus	sp.A	2A	4	1	2		2
		Syringolaimus	sp.B	2A	3			2	
		Syringolaimus?		2A	?				1
		Thalassironus	sp.A	1A	4				1
	OXYSTOMINIDAE	Criccohalalaimus?		1A	4				1
		Halalaimus	sp.D	1A	4			2	
		Halalaimus	sp.E	1A	4	1	1	1	1
		Halalaimus	sp.F	1A	4	1			1
		Halalaimus	sp.G	1A	4				1
		Halalaimus	sp.H	1A	4	1			
		Litinium	sp.A	1A	1			1	
		Oxystomina	sp.A	1A	4		1		
		Wieseria	sp.A	1A	4			2	
	ONCHOLAIMIDAE	*Adoncholaimus*?		2B	3	1			
		Viscosia?	sp.A	2B	3	1			
	ENCHELIDIIDAE	Bathyeurystomina	sp.A	2B	4		1		
	TRIPYLOIDIDAE	Tripyloides	sp.A	2B	3		1		
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp.D	2A	4	5	2	4	1
		Acantholaimus	sp.E	2A	4		1	4	2
		Acantholaimus	sp.F	2A	4				1
		Acantholaimus?		2A	?				1
		Actinonema	sp.A	2A	3		1	3	1

	Chromadorella	sp.A	2A	3				1
	Endeolophus	sp.A	2A	3		1		1
	Prochromodorella?		2A	3			1	2
	Rhips?		2A	3			3	1
	Rhips	sp.A	2A	3				1
COMESOMATIDAE	Cervonema	sp.A	1A	3				1
	Laimella?		1A	3		1		
CYATHOLAIMIDAE	Paracyatholaimoides?		2A	3			1	
SELACHINEMATIDAE	Halichoanolaimus	sp.A	2B	4				1
DESMODORIDAE	Desmodora	sp.C	2A	3		1		
	Desmodora	sp.D	2A	3	2		1	1
DRACONEMATIDAE	Eudraconema	sp.A	2A	3	1	3		
MICROLAIMIDAE	Aponema	sp.A	2A	3	4	5	4	4
	Microlaimidae	sp.E	2A	3				1
	Microlaimidae	indet.	2A	3	1		1	2
	Microlaimus	sp.A	2A	3		8	2	
	Microlaimus	sp.B	2A	3	4	7	2	2
	Molgolaimus	sp.A	2A	3	4	4	7	4
	Molgolaimus	sp.B	2A	3	4	1		
	Nox	sp.B	2A	3	2	2	3	
LEPTOLAIMIDAE	Leptolaimidae?		1A	4	1	1		
	Leptolaimus	sp.B	1A	3		1		
	Leptolaimus	sp.C	1A	3	1			
	Leptolaimus	sp.D	1A	3	1			
AEGIALOALAIMIDAE	Aegialoalaimus	sp.A	1A	1				1
	Diplopeltoides	sp.D	1A	3	1			
	Diplopeltoides	sp.E	1A	3	1	5	1	3
	Southernia	sp.A	1A	2			1	1
TUBOLAIMOIDIDAE	Chitwoodia	sp.B	1A	3		1	1	
	Tubolaimoides	sp.A	1A	3	1	1		
CERAMONEMATIDAE	Pselionema	sp.A	1A	3		1		
	Pselionema	sp.B	1A	3	1	1		
	Pselionema	sp.C	1A	3			1	
MEYLIIDAE	Quadricoma	sp.A	1A	3	3	2	1	3

	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	3	1	1	1
		Desmoscolex	sp.B	1A	3	4	1	3	3
		Desmoscolex	sp.C	1A	3	1			
		Desmoscolecidae		1A	3	1	1	2	2
		Amphidless gen nov		1A	3			1	
MONHYSTERIDA	MONHYSTERIDAE	Geomonhystera?	sp.A	1A	4			1	
		Geomonhystera	sp.A	1A	4	1			
		Geomonhystera	sp.B	1A	4	1			
		Monhysteridae?		1A	4	1		1	4
		Monhysteridae	sp.F	1A	4	4	3	4	5
		Monhysteridae	sp.G	1A	4			1	
		Thalssomonhystera	sp.A	1A	4	2	2	4	7
		Thalssomonhystera	sp.B	1A	4	1	1	4	3
		Thalssomonhystera	sp.C	1A	4	9	5	4	3
		Thalssomonhystera	sp.D	1A	4	6	6	1	6
		Thalssomonhystera	sp.E	1A	4	1	1	4	7
		Thalssomonhystera	sp.F	1A	4	1			3
	XYALIDAE	Amphimonhystera	sp.C	1A	4		1		
		Capsula	sp.A	1B	3		1		
		Elzalia?		1B	3	1			
		Linhystera?		1A	4		1	2	2
		Manganonema	sp.A	1A	4	4		1	
		Theristus?		1B	3		1	1	
		Xyalidae?		1B	3				1
		Xyalidae	sp.A	1A	3	1	3		
		Xyalidae	sp.B	1B	3			2	
		Xyalidae	sp.C	1A	3			2	1
		Xyalidae	sp.D	1B	3				1
	LINHOMOEIDAE	Linhomoeidae?		1B	4	2		1	
	AXONOLAIMIDAE	Ascolaimus?	sp.A	1A	3	5		2	1
	DIPLOPELTIDIDAE	Campylaimus	sp.B	1A	2	1		1	1
		Campylaimus	sp.C	1A	2		1	1	
		Campylaimus	sp.D	1A	2			1	
		Diplopeltula	sp.B	1A	2			1	

Diplopeltula	sp.C	1A	2	1					
Southerniella	sp.B	1B	3	1					2
Indet 1		1A	3	1					
Indet 3			4	1					
Indet 4		2A	4		1				
Indet 6		1B	3						1
unkn (chromadorid)						1			
unkn							1		

Station: 5°N
Surface 0-1cm

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC15 V17	BC16 V17	BC 17 V12	BC18 V17	MC26 Tube 7
ENOPLIDA	ENOPLIDAE	Trichenoplus	sp.A	2B	3			1		
	THORACOSTOMOPSIDAE	*Enolpoides?*		2B	3		1			
		Mesacanthion	sp.A	2B	3	1				
		Paramesacanthion	sp.A	2B	4					1
	PHANODERMATIDAE	Micoletzkyia?		1A	3				1	
		Phanodermopsis	sp.A	1A	3				1	
		Viscosia	sp.A	1A	4				2	
		Phanodermatidae	sp.A	1A	4	1				
		Phanodermatidae	sp.B	1A	3			1		
	IRONIDAE	Syringolaimus	sp.B	2A	4	1		1		1
		Syringolaimus	sp.C	2A	4	1	2		1	
		Syringolaimus	sp.D	2A	4			1		
		Thalassironus	sp.A	2A	4			2		
		Thalassironus	sp.B	2A	4			1		
	OXYSTOMINIDAE	Halalaimus	sp.H	1A	4	2	1	1		2
		Halalaimus	sp.I	1A	4			1		
		Halalaimus	sp.K	1A	4		3		5	
		Halalaimus	sp.J	1A	4	1		1		
		Litinium	sp.B	1A	1	1		1		
		Oxystomina	sp.A	1A	4			2		1
		Oxystomina	sp.B	1A	4			1		
	ONCHOLAIMIDAE	Pontonema?	sp.A	2B	3					1
	ENCHELIDIIDAE	Bathyeurystomina	sp.A	2B	4		2			
CHROMADORIDA	CHROMADORIDAE	Acantholaimus?		2A	4	1			3	1
		Acantholaimus	sp.F	2A	4	1	4	2	5	7
		Acantholaimus	sp.G	2A	4			1		1
		Acantholaimus	sp.H	2A	4	4	1	3	3	3
		Actinonema	sp.A	2A	3			1	2	
		Endeolophus	sp.A	2A	3				1	

	Neochromadora	sp.A	2A	3	1			2	
	Rhips	sp.A	2A	3			1		1
COMESOMATIDAE	Cervonema?		1A	3				1	1
	Cervonema	sp.B	1A	4		2	1	2	
	Cervonema	sp.C	1A	2				1	
	Laimella?		1A	3					2
CYATHOLAIMIDAE	Cyatholaimidae	sp.A	2A	3					2
	Marylynnia	sp.A	2A	4			1		
	Marylynnia	sp.B	2A	4					1
	Marylynnia?		2A	4					1
	Paracanthonchus?		2A	3				1	1
	Pomponema?		2A	3				1	
DESMODORIDAE	Desmodora	sp.E	2A	4	1		4		1
	Desmodora	sp.F	2A	3	1	3	1		1
	Desmodora?		2A	3			1		
DRACONEMATIDAE	Eudraconema	sp.A	2A	3	1		2		
MICROLAIMIDAE	Aponema	sp.A	2A	3	2	2	2	4	2
	Aponema	sp.B	2A	3	3		1	5	
	Microlaimidae?		2A	3			1		
	Microlaimidae	sp.G	2A	3		1			
	Microlaimus	sp.A	2A	3	2	2	1	2	3
	Microlaimus	sp.B	2A	3		1		1	1
	Microlaimus	sp.C	2A	3	2	3	7	2	1
	Molgolaimus	sp.B	2A	3	7	4	10	3	9
	Molgolaimus	sp.C	2A	3				4	2
	Molgolaimus	sp.D	2A	3			1		
LEPTOLAIMIDAE	Camacolaimus	sp.B	2A	3			1		
	Leptolaimus	sp.E	1A	4	1	2			2
	Leptolaimus	sp.F	1A	3	1				
	Leptolaimus	sp.G	1A	3			3	2	
	Leptolaimidae?		1A	3					1
AEGIALOALAIMIDAE	Aegialoalaimidae?		1A	3		1			
	Aegialoalaimus	sp.B	1A	1		1			
	Cyartonema	sp.A	1A	2				1	
	Diplopeltoides	sp.F	1A	3	2	2			4

	Diplopeltoides	sp.G	1A	3		3			
	Southernia	sp.B	1A	3			1	1	
TUBOLAIMOIDIDAE	Tubolaimoides	sp.A	1A	3	2	3	1	1	1
CERAMONEMATIDAE	Pselionema	sp.A	1A	3			1	1	1
	Pselionema	sp.B	1A	3			1		
MEYLIIDAE	Quadricoma	sp.A	1A	3	3	3	1	3	
	Quadricoma	sp.B	1A	3	1		2		
	Quadricoma?		1A	3	1	3			
DESMOSCOLECIDAE	Amphidless gen nov	sp.A	1A	3	12	4	2	1	5
	Desmoscolex	sp.A	1A	3	2	1	2		
	Desmoscolecidae		1A	3	1				
MONHYSTERIDAE	Monhysteridae indet		1A	?		1			1
	Monhysteridae	sp.H	1A	3	1	2	1	1	1
	Monhysteridae	sp.I	1A	4	3	4			3
	Monhysteridae	sp.J	1A	4		1			
	Thalassomonhystera	sp.G	1A	4	1	3	2	2	6
	Thalassomonhystera	sp.H	1A	3	11	12	7	9	11
	Thalassomonhystera	sp.I	1A	4		1	1	3	1
	Thalassomonhystera	sp.J	1A	4	6	2	4	5	2
	Thalassomonhystera	sp.K	1A	4	3	1	1	2	1
	Thalassomonhystera	sp.L	1A	4	2	2			
	Thalassomonhystera	sp.M	1A	4	1	2	1		
	Thalassomonhystera?		1A	4				2	1
XYALIDAE	Amphimonhystera	sp.D	1A	4	1				
	Daptonema	sp.A	1B	4	1			1	1
	Linhystera	sp.B	1A	4					1
	Linhystera	sp.C	1A	4	2		1	1	
	Manganonema	sp.B	1A	3	3	1	1	2	
	Manganonema	sp.C	1A	3		1			
	Manganonema	sp.D	1A	3			1		
	Xyalidae?		1A	4		1		1	4
	Xyalidae	sp.D	1A	3					1
	Xyalidae	sp.E	1A	4	2	1			
	Xyalidae	sp.F	1A	4	1				1
	Xyalidae	sp.G	1B	4	1				

	Xyalidae	sp.H	1A	4			2	1	
LINHOMOEIDAE	Anticyathus?		1B	3					1
AXONOLAIMIDAE	Ascolaimus	sp.A	1A	3					1
	Ascolaimus	sp.B	1A	3	1	5		1	1
	Ascolaimus	sp.C	1A	3				1	
DIPLOPELTIDIDAE	Campylaimus?		1A	2		1		1	
	Campylaimus	sp.C	1A	2		1			
	Campylaimus	sp.D	1A	2				1	1
	Diplopeltidae		1A	3		1			
	Diplopeltula	sp.A	1A	3			1	1	
	Diplopeltula?		1A	3					1
	Pararaeolaimus	sp. A	1A	3		1	1		
	Southerniella	sp.B	1B	3					2
	Indet 1		2A	4		1			
	Indet 3		1B	3	1				
	Indet 4		1A	4			1		
	Indet 5		1A					1	
	Indet 6		1A	4				1	
	Indet 7							1	

Station: 9°N
Surface 0-1cm

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC19 V20	BC20 V16	BC22 V12
ENOPLIDA	IRONIDAE	Doliocholaimus	sp.A	2A	3	1		
		Syringolaimus? indet juv		2A	4	2	1	1
	OXYSTOMINIDAE	Halalaimus	sp.A	1A	4	1		2
		Halalaimus	sp.B	1A	4	3	1	
		Halalaimus	sp.C	1A	4	2	1	
		Halalaimus	sp.D	1A	4	1		
		Halalaimus	sp.E	1A	4		1	2
		Halalaimus	sp.F	1A	4			1
		Halalaimus?		1A	4			1
		Litinium	sp.A	1A	1		2	
		Oxystomina	sp.B	1A	4	1		
	ONCHOLAIMIDAE	Metoncholaimus?		2B	3		1	
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp.A	2A	4	6	4	4
		Acantholaimus	sp.B	2A	4	2		
		Acantholaimus?		2A	4	1		1
		Actinonema	sp.A	2A	3	1		
		Chromadora?		2A	3			2
		Prochromadorella	sp.A	2A	3	2	2	1
	COMESOMATIDAE	Cervonema	sp.A	2A	3		1	
	CYATHOLAIMIDAE	Cyatholaimus	sp.A	2A	3		1	
		Marylynnia	sp.A	2A	4			1
		Paracanthonchus?		2A	3	1	1	
		Paracyatholaimoides?		2A	4	1		
		Pomponema?		2A	4	1		
	DESMODORIDAE	Desmodora	sp.A	2A	3	1	2	
		Desmodora	sp.B	2A	3		1	
		Desmodora	sp.C	2A	3		1	
		Paradesmodora	sp.A	2A	3	1		1

	DRACONEMATIDAE	Eudraconema	sp.A	2A	3	1		
	MICROLAIMIDAE	Microlaimus	sp.A	2A	3	6		4
		Microlaimus	sp.B	2A	3		1	
		Molgolaimus	sp.A	2A	3	2		2
		Nox	sp.A	2A	3		2	1
		Paramicrolaimus	sp.A	2A	3			1
	LEPTOLAIMIDAE	Camacolaimus	sp.B	2A	3	1		
		Leptolaimus	sp.A	1A	3	3		
		Leptolaimus	sp.B	1A	4	3	2	
		Leptolaimus	sp.C	1A	3	1		2
	AEGIALOALAIMIDAE	Aegialoalaimus	sp.A	1A	1	1	3	2
		Cyartonema?		1A	2		1	
		Diplopeltoides	sp.A	1A	3		1	1
		Diplopeltoides	sp.B	1A	3		3	
		Diplopeltoides?		1A	3			1
		Southernia	sp.A	1A	3			1
	CERAMONEMATIDAE	Pselionema	sp.B	1A	3			1
	TUBOLAIMOIDIDAE	Chitwoodia	sp.A	1A	3			1
	MEYLIIDAE	Quadricoma	sp.A	1A	3		2	3
		Quadricoma	sp.B	1A	3			1
	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	1		
		Desmoscolex	sp.B	1A	3	1		1
		Desmoscolecidae		1A	3	2	1	4
		Amphidless? gen nov		1A	3		1	1
MONHYSTERIDA	MONHYSTERIDAE	Monhysteridae	sp.A	1A	3	2	4	7
		Monhysteridae	sp.B	1A	4	1	1	
		Monhysteridae	sp.C	1A				1
		Thalssomonhystera	sp.A	1A	4	7	14	4
		Thalssomonhystera	sp.B	1A	4	6	13	3
		Thalassomonhystera	sp.C	1A	3	5	1	1
		Thalssomonhystera	sp.D	1A	4	5	12	4
		Thalassomonhystera	sp.E	1A	4	1	3	3
		Thalassomonhystera	sp.F	1A	4	1	2	3
		Thalassomonhystera	sp.?	1A	4	1		

XYALIDAE	Amphimonhystera	sp.A	1B	4		1	2
	Amphimonhystrella	sp.A	1B	4	1		
	Cobbia	sp.A	2A	4	2	1	1
	Cobbia	sp.B	2A	4			1
	Cobbia?		2A	4		1	1
	Daptonema	sp.A	1B	3	1		
	Linhystera	sp.A	1A	3		2	5
	Linhystera?		1A	3			2
	Manganonema	sp.A	1A	3	3		2
	Manganonema	sp.B	1A	3	1	1	
	Manganonema?		1A	3	1		
	Paramonhystera?		1B	3	1		
	Theristus	sp.A	1B	3			2
	Xyalidae?	sp.A	2A		1		
	Xyalidae	sp.A	1A			2	
	Xyalidae	sp.B	1A				1
	Xyalidae	sp.C	1B				1
LINHOMOEIIDAE	Linhomoeiidae?		1B	3	2		1
SPHAEROLAIMIDAE	Sphaerolaimus	sp.A	2B	3			1
AXONOLAIMIDAE	Ascolaimus	sp.A	1A	3	1		
	Ascolaimus	sp.B	1A	3	1		
DIPLOPELTIDIDAE	Araeolaimus?		1A	3	1		
	Campylaimus	sp.A	1A	2	1		
	Campylaimus	sp.B	1A	2		1	
	Camplaimus/Diplopeltula		1A	2	1		
	Diplopeltula	sp.A	1A	3		4	3
	Southernella	sp.A	1A	3			1

Station: 23°N
Surface 0-1cm

Order	Family	Genus	Species	Feeding Group	Tail Shape	MC1 Tube 8	MC2 Tube 4	MC4 Tube 6	MC6 Tube 2
ENOPLIDA	THORACOSTOMOPSIDAE	Enoploides?		2B	3	1			
		Mesacanthion	sp.A	2B	3			2	
	PHANODERMATIDAE	Phanodermatidae		1A	4		1		1
		Phanodermopsis	sp.A	1A	3		1		
	IRONIDAE	Syringolaimus? indet juv		2A	4				2
	OXYSTOMINIDAE	Halalaimus	sp.A	1A	4	3	1	2	2
		Halalaimus	sp.B	1A	4		1	1	
		Halalaimus	sp.C	1A	4		2	1	1
		Halalaimus	sp.E	1A	4	1	2		3
		Halalaimus	sp.F	1A	4				1
		Oxystomina	sp.B	1A	4	1			
		Wieseria	sp.A	1A	4			1	
	ENCHELIIDAE	Bathyeurystomina	sp.A	2B	4		1	1	1
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp.A	2A	4	3	1	3	4
		Acantholaimus	sp.B	2A	4	1	1	2	1
		Acantholaimus	sp.C	2A	3	7	3	3	
		Actinonema	sp.A	2A	3		1	2	1
		Hypodontolaimus?		2A	3		1		
		Neochromadora?	sp.A	2A	3	1	2	1	1
		Prochromadorella?	sp.A	2A	3	1	1	1	
	COMESOMATIDAE	Cervonema	sp.A	2A	3	1			
		Cervonema	sp.B	2A	3	1			
	CYATHOLAIMIDAE	Cyatholaimus	sp.A	2A	3				3
		Paracanthonchus?		2A	3				1
		Paracyatholaimoides?		2A	4			1	
		Pomponema?		2A	4				1
	DESMODORIDAE	Desmodora	sp.A	2A	3			1	1
		Desmodora	sp.B	2A	3	1			

		Desmodora	sp.C	2A	3		1		
	DRACONEMATIDAE	Eudraconema	sp.A	2A	3		1		1
	MICROLAIMIDAE	Microlaimidae indet		2A	3	1			
		Aponema	sp.A	2A	3		5	6	3
		Microlaimus	sp.A	2A	3	4	2	3	5
		Molgolaimus	sp.A	2A	3	2			
		Molgolaimus	sp.B	2A	3	1			1
		Nox	sp.A	2A	3			1	1
	LEPTOLAIMIDAE	Camacolaimus	sp.B	2A	3			1	1
		Dennis gen nov	sp.A	1A	3		1		1
		Leptolaimus	sp.B	1A	4		2		
		Leptolaimus	sp.C	1A	3	2	2		6
		Leptolaimus	sp.D	1A	3	1		1	
		Strange Chromadorid		1A	4	1			
	AEGIALOALAIMIDAE	Aegialoalaimus	sp.A	1A	1	3	5	1	1
		Cyartonema?		1A	2			2	
		Diplopeltoides	sp.A	1A	3		2	1	2
		Diplopeltoides	sp.B	1A	3			1	1
	CERAMONEMATIDAE	Pselionema	sp.A	1A	3	1	2	2	
	TUBOLAIMOIDIDAE	Chitwoodia	sp.A	1A	3				1
		Tubolaimoides	sp.A	1A	3			1	
	MEYLIIDAE	Greefiella	sp.A	1A	3	2			
		Quadricoma	sp.A	1A	3	1			
		Quadricoma	sp.B	1A	3	1	3		
	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	2		2	
		Desmoscolex	sp.B	1A	3	2	1		
		Amphidless? gen nov		1A	3	1	1		1
MONHYSTERIDA	MONHYSTERIDAE	Monhysteridae	sp.A	1A	3	4			
		Monhysteridae indet		1A	?	1	1		
		Thalassomonhystera	sp.A	1A	4	10	12	7	9
		Thalassomonhystera	sp.B	1A	4	11	18	9	15
		Thalassomonhystera	sp.C	1A	3	3	2	3	5
		Thalassomonhystera	sp.D	1A	4	5		7	3
		Thalassomonhystera	sp.E	1A	4		1	1	
		Thalassomonhystera	sp.F	1A	4	1	2	1	3

XYALIDAE	Amphimonhystera?	sp.A	1B	4		1		
	Amphimonhystrella	sp.A	1B	4			1	
	Capsula	sp.A	1B	3			2	1
	Cobbia	sp.A	2A	4	1			
	Daptonema	sp.A	1B	4	1	2	2	1
	Daptonema	sp.B	1B	4		1		
	Daptonema	sp.C	1B	4		1		1
	Linhystera	sp.A	1A	3	6	6	11	3
	Manganonema	sp.A	1A	3	1	1	2	4
	Metadesmolaimus	sp.A	1B	3	1			3
	Paramonhystera	sp.A	1B	3		2		1
	Theristus	sp.A	1B	3	6		9	1
	Xyalidae	sp.A	1A		1			
	Xyalidae	sp.B	1A		1			1
SPHAEROLAIMIDAE	Sphaerolaimus	sp.A	2B	3			1	
DIPLOPELTIDIDAE	Campylaimus	sp.B	1A	2	1	1	2	1
	Campylaimus/Diplopeltula		1A	3		1		
	Southerniella	sp.A	1A	3	1	2		1
			Total		102	101	102	102

Station: Equator
Whole core (0-5cm)

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC4 V6 0-1cm	1-2cm	2-3cm	3-5cm	BC6 V14 0-1cm	1-2cm	2-3cm	3-5cm	BC8 V16 0-1cm	1-2cm	2-3cm	3-5cm
ENOPLIDA	THORACOSTOMOPSIDAE	Mesacanthion?		2B	3										1		
		Paramesacanthion	sp.A	2B	3					2							
	ANOPLOSTOMATIDAE	Anoplostoma	sp.A	1B	4				1		1						
	PHANODERMATIDAE	Phanodermatidae	sp.A	1A	3	1											
		Phanodermatidae	sp.B	1A	4	1										1	
		Crenopharynx?		1A	3										1		
	IRONIDAE	Syringolaimus	sp.A	2A	3					1		4	5		1	1	2
		Syringolaimus	sp.B	2A	3					1	1				1		
		Syringolaimus indet juv		2A	4		2	21	73		1	2				1	3
	OXYSTOMINIDAE	Halalaimus	sp.A	1A	4									1	1	1	
		Halalaimus	sp.B	1A	4					1			1			1	
		Halalaimus	sp.C	1A	4			1		3	2	2					
		Halalaimus	sp.D	1A	4	2				1	2			1	2	1	1
		Halalaimus	sp.E	1A	4						3	1					
		Litinium	sp.A	1A	1						1	4	1	1	1	2	3
		Litinium	sp.B	1A	3	1						2	2		3		
		Oxystomina	sp.A	1A	2											1	1
		Oxystomina?		1A	2					1							
		Thalassolaimus	sp.A	1B	3					1							
	ONCHOLAIMIDAE	Viscosia	sp.A	2B	3			1									1
		Viscosia?		2B	3	2	1	2					2				
		Metoncholaimus?		2B	3									1			
		Metaparaoncholaimus?		2B	4	1											
		Oncholaimus?		2B	1		1		2			1					
		Pontonema?		2B	1		1										
		Oncholaimidae indet		2B	3					1							
	ENCHELIDIIDAE	Bathyeurystomina	sp.A	2B	4	1				1			1		1		
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp. indet	2A	4						1			1	1		
		Acantholaimus	sp.A	2A	4	3		2		5	8	2	7	2	1	4	1
		Acantholaimus	sp.B	2A	4	2				3	1	1	1	4	3		
		Acantholaimus	sp.C	2A	3	1				1			1		4		
		Acantholaimus	sp.D	2A	4	1							1			1	2
		Actinonema	sp.A	2A	3	1				2	1			4		1	
		Chromadorella?	sp.A	2A	3		1										
		Prochromadorella	sp.A	2A	3					1					1	1	1
		Prochromadorella?		2A	3							1			1	1	
	COMESOMATIDAE	Cervonema	sp.A	1A	3							1					

	Cervonema?		1A	3	1					2								
CYATHOLAIMIDAE	Cyatholaimidae	sp.A	2A	3						1								
	Cyatholaimidae indet		2A	?														1
	Cyatholaimus	sp.A	2A	3		5	4	1				1				1	2	1
	Marylynnia	sp.A	2A	4						1								1
	Marylynnia	sp.B	2A	4														1
	Marylynnia?		2A	4									2				1	
	Paracanthonchus?		2A	3											1			
DESMODORIDAE	Desmodora	sp.A	2A	3	1					1	1				2	1	1	
	Desmodora	sp.B	2A	3											1			
	Desmodora	sp.C	2A	3						3								
	Desmodora	sp.D	2A	3						1					1			
	Paradesmodora?		2A	3											1			
DRACONEMATIDAE	Eudraconema	sp.A	2A	3						1								
MICROLAIMIDAE	Aponema	sp.A	2A	3	1					1	1				1	2		
	Microlaimidae indet		2A	3														1
	Microlaimus	sp.A	2A	3			1								1			
	Microlaimus	sp.B	2A	3	3					1					1			
	Molgolaimus	sp.A	2A	3							2					4	3	3
	Molgolaimus	sp.B	2A	3						1								
	Molgolaimus	sp.D	2A	3											1			
	Nox	sp.A	2A	3						1								
LEPTOLAIMIDAE	Antomicron	sp.A	1A	3	1													
	Camacolaimus	sp.A	2A	3	1	3	1				1				1		1	
	Camacolaimus	sp.B	2A	3		2	2					3	5			1	3	8
	Dennis gen nov	sp.A	1A	3											1			
	Leptolaimus	sp.A	1A	3						2	1				2			
	Leptolaimus	sp.B	1A	3	1						2				2		1	
	Leptolaimus	sp.C	1A	3	1		1	2		1	3	1	2			3		
	Leptolaimus	sp.D	1A	3												1	2	
	Leptolaimus	sp.E	1A	3						1								
	Leptolaimus/Stephanolaimus		1A	3	1													
	Strange Chromadorid	juv	1A	4		2	6					1				1	1	
AEGIALOALAIMIDAE	Aegialoalaimus	sp.A	1A	1							1	2	2					
	Cyartonema?		1A	2											1			
	Diplopeltiodes	sp.A	1A	3						2					1	1		
	Diplopeltoides	sp.B	1A	3			1			3	5	2	3		5	3	1	2
	Diplopeltoides	sp.C	1A	3							1		2		1			
	Diplopeltoides	sp.D	1A	3												2	1	
	Southernia	sp.A	1B	3				1		1								
TUBOLAIMOIDIDAE	Chitwoodia	sp.A	1A	3											1			
	Tubolaimoides	sp.A	1A	3						1								
CERAMONEMATIDAE	Pselionema	sp.A	1A	3							2				1			

		Pselionema	sp.B	1A	3					1								
	MEYLIIDAE	Greefiella	sp.A	1A	3								1			1	2	
		Quadricoma	sp.A	1A	3		1	1		2	3	2	8	3	6			
		Quadricoma	sp.B	1A	3	1		1			2	1	2	2		2		
		Quadricoma	sp.C	1A	3	3				1		2		3	3	3	1	
		Tricoma/Quadricoma?		1A	3	1				1								
	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	1				1	5	1	1	1			27	
		Desmoscolex	sp.B	1A	3					1	1	3	2	1	1	2	6	
		Desmoscolex	sp.C	1A	3	2			1									
		Desmoscolex?		1A	3	1								1				
		Desmoscolecidae	sp.A	1A	3	2		1			1	1						
		Amphidless gen nov	sp.A	1A	3								1	1	2	3	2	
MONHYSTERIDA	MONHYSTERIDAE	Monhysteridae?		1A	4	2				2				2				
		Monhysteridae	sp.A	1A	4	1				1				9				
		Monhysteridae	sp.B	1A	4	1				2				1				
		Monhysteridae	sp.C	1A	4	4				5				1				
		Monhysteridae	sp.D	1A	4	1				7				1				
		Monhysteridae	sp.E	1A	4									1				
		Thalassomonhystera	sp.?	1A	4						1			1				
		Thalassomonhystera	sp.A	1A	4	2				5	8	7	2	8	10	21	2	
		Thalassomonhystera	sp.B	1A	4	10		2		6	7	10	18	5	9	10	6	
		Thalassomonhystera	sp.C	1A	4					1				1				
		Thalassomonhystera	sp.D	1A	4	2	4	11	8	4	10	12	5	2	13	4	3	
		Thalassomonhystera	sp.E	1A	4	1	1			1	6	4	2				1	
		Thalassomonhystera	sp.F	1A	4					1	1	2	3		2	3	1	
		Thalassomonhystera	sp.G	1A	4		7											
		Thalassomonhystera	sp.H	1A	4		1											
	XYALIDAE	Amphimonhystera	sp.A	1A	4									1				
		Amphimonhystera	sp.B	1A	4									1	1			
		Cobbia	sp.A	1A	4		60	11	9		4	13	10		4	2	1	
		Cobbia?		1A	4									1				
		Linhystera	sp.A	1A	4	1					2	4	1	1	1	1	4	
		Manganonema	sp.A	1A	4	2	1	3	1	1	3	2	2	3	3	2	1	
		Metadesmolaimus?		1B	3									1				
		Paramonhystera?		1B	3							1						
		Theristus	sp.A	1B	3						1	1			1			
		Xyalidae?		1B	3		5			1								
		Xyalidae	sp.A	1A	4									1				
		Xyalidae	sp.C	1A	3					1								
		Xyalidae	sp.D	1A	3									1				
		Xyalidae	sp.E	1B	4	1				1								
	LINHOMOEIIDAE	Paralinhomoeus?		1B	3					1								
	SPHAEROLAIMIDAE	Metasphaerolaimus	sp.A	2B	1						1			1				

	Metasphaerolaimus	sp.B										1				
AXONOLAIMIDAE	Ascolaimus	sp.A	1A	3			1			1					2	9	2
	Axonolaimus?		1B	3		1											
DIPLOPELTIDIDAE	Araeolaimus?	sp.A	1A	2		2					1					3	1
	Campylaimus	sp.A	1A	2											1	1	
	Campylaimus	sp.B	1A	2	1											1	1
	Diplopeltula	sp.A	1A	3	1					1	1	1					1
	Diplopeltula	sp.B	1A	3									1				1
	Diplopeltua	sp.C	1A	3									3				
	Pararaeolaimus	sp. A	1A	3	1												
	Southerniella	sp.A	1B	3												2	1
	Indet 1		1A	3	1												
	Indet 3		2A	3	1												
	Indet 6		1A	4	1												
	Unkn		1A	3	2			1									

Station: 5°N
Whole Core (0-5cm)

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC15 V17 0-1cm	1-2cm	2-3cm	3-5cm	BC16 V17 0-1cm	1-2cm	2-3cm	3-5cm	BC17 V15 0-1cm	1-2cm	2-3cm	3
ENOPLIDA	ENOPLIDAE	Trichenoplus	sp.A	2B	3		1							1			
	THORACOSTOMOPSIDAE	Enoploides?		2B	3					1							
		Mesacanthion	sp.A	2B	3	1											
		Paramesacanthion	sp.A	2B	4						1						
		Paramesacanthion?		2B	4			1									
	ANOPLOSTOMATIDAE	Anoplostoma?		1B	4			1	2								
	PHANODERMATIDAE	Phanodermopsis?		1A	3			2			1				2		
		Phanodermopsis	sp.A	1A	3		1										
		Viscosia?		1A	3						1				1		
		Phanodermatidae	sp.A	1A	4	1					2						
		Phanodermatidae	sp.B	1A	3									1			
	IRONIDAE	Syringolaimus	sp.B	2A	4	1			2			2		1			
		Syringolaimus	sp.C	2A	4	1				2		2	3			3	
		Syringolaimus	sp.D	2A	4									1			
		Syringolaimus indet juv		2A	4		1	10	9		2	25	3		1	26	
		Thalassironus	sp.A	2A	4									2		3	
		Thalassironus	sp.B	2A	4									1			
	OXYSTOMINIDAE	Halalaimus	sp.H	1A	4	2	2			1				1	1		
		Halalaimus	sp.I	1A	4									1			
		Halalaimus	sp.K	1A	4					3	1						
		Halalaimus	sp.J	1A	4	1	1	1						1	1		
		Litinium	sp.A	1A	1				2								
		Litinium	sp.B	1A	1	1								1	1	1	
		Litinium	sp.C	1A	3		1				1						
		Oxystomina	sp.A	1A	4									2			
		Oxystomina	sp.B	1A	4									1			
		Oxystomina?		1A	4		1										
	ONCHOLAIMIDAE	Adoncholaimus?		2B	3											1	
	ENCHELIDIIDAE	Bathyeurystomina	sp.A	2B	4					2	1				1	1	
CHROMADORIDA	CHROMADORIDAE	Acantholaimus?		2A	4	1											
		Acantholaimus	sp.F	2A	4	1	6	3	2	4	3	1	1	2	6	2	
		Acantholaimus	sp.G	2A	4		1	1			1			1			
		Acantholaimus	*sp.H*	2A	4	4	11	6	9	1	4	3	5	3	5	1	
		Acantholaimus indet		2A	?				1								
		Actinonema	sp.A	2A	3		3	1						1	2	1	
		Chromadorella?		2A	3		1						1			1	
		Neochromadora	sp.A	2A	3	1											

	Rhips	sp.A	2A	3									1			
COMESOMATIDAE	Cervonema	sp.B	1A	4		3	1		2	1			1	2	2	
	Cervonema	sp.C	1A	2		1								1		
CYATHOLAIMIDAE	Cyatholaimus	sp.A	2A	3			5			2	1	2		4	2	
	Marylynnia	sp.A	2A	4								1	1		1	
	Paralongicyatholaimu	sp.A	2A	4											1	
	Pomponema?		2A	3			1									
DESMODORIDAE	Desmodora	sp.E	2A	4	1					1			4			
	Desmodora	sp.F	2A	3	1				3				1			
	Desmodora	sp.G	2A	3		1	1				1					
	Desmodora?		2A	3									1			
DRACONEMATIDAE	Eudraconema	sp.A	2A	3	1								2			
MICROLAIMIDAE	Aponema	sp.A	2A	3	2	1			2	3			2			
	Aponema	sp.B	2A	3	3			1		3			1	1		
	Microlaimidae?		2A	3									1			
	Microlaimidae	sp.G	2A	3					1							
	Microlaimus	sp.A	2A	3	2	1	1		2	1		1	1			
	Microlaimus	sp.B	2A	3					1							
	Microlaimus	sp.C	2A	3	2				3				7			
	Molgolaimus	sp.B	2A	3	7				4				10			
	Molgolaimus	sp.D	2A	3									1			
LEPTOLAIMIDAE	Camacolaimus	sp.B	2A	3				1			5	3	1			
	Leptolaimus	sp.D	1A	3										1	1	
	Leptolaimus	sp.E	1A	4	1	2	1	1	2	2	3	4			1	
	Leptolaimus	sp.F	1A	3	1	1										
	Leptolaimus	sp.G	1A	3			1			1			3		1	
	Strange chromadorid		1A	4		1		1				1			5	
AEGIALOALAIMIDAE	Aegialoalaimidae?		1A	3					1							
	Aegialoalaimus	sp.A	1A	1				1		3		1				
	Aegialoalaimus	sp.B	1A	1			1		1							
	Cyartonema	sp.A	1A	2			2			2						
	Diplopeltoides	sp.F	1A	3	2	2	2	2	2	1	1			1		
	Diplopeltoides	sp.G	1A	3		1	1	1	3		1	1				
	Southernia	sp.B	1A	3									1	1		
TUBOLAIMOIDIDAE	Tubolaimoides	sp.A	1A	3	2	1	1		3	2			1		1	
CERAMONEMATIDAE	Pselionema	sp.A	1A	3									1			
	Pselionema	sp.B	1A	3									1			
MEYLIIDAE	Greefiella	sp.A	1A	3		1										
	Quadricoma	sp.A	1A	3	3	3			3	2			1			
	Quadricoma	sp.B	1A	3	1								2			
	Quadricoma?		1A	3	1				3							
DESMOSCOLECIDAE	Amphidless gen nov	sp.A	1A	3	12	4	4		4	2		2	2	1		
	Desmoscolex	sp.A	1A	3	2	2	2		1				2			

		Desmoscolecidae		1A	3	1										1	
MONHYSTERIDA	MONHYSTERIDAE	Monhysteridae indet		1A	?					1							
		Monhysteridae	sp.H	1A	3	1				2					1		
		Monhysteridae	sp.I	1A	4	3				4							
		Monhysteridae	sp.J	1A	4					1							
		Thalassomonhystera	sp.G	1A	4	1	11	10	15	3	22	27	14	2	10	13	
		Thalassomonhystera	sp.H	1A	3	11	1	3		12	1	3	2	7			
		Thalassomonhystera	sp.I	1A	4		1	2		1				1		1	
		Thalassomonhystera	sp.J	1A	4	6	8	17	6	2	12	11	10	4	8	10	
		Thalassomonhystera	sp.K	1A	4	3	2	3	2	1				1	8	3	
		Thalassomonhystera	sp.L	1A	4	2	4			2		4	1		1	3	
		Thalassomonhystera	sp.M	1A	4	1	5	4		2	4	1		1		1	
		Thalassomonhystera	indet	1A	4		2										
	XYALIDAE	Amphimonhystera	sp.D	1A	4	1	2				2	1			1	5	
		Capsula	sp.A	1B	3							1					
		Cobbia	sp.A	1A	4		1	3	5				1		33	6	
		Daptonema	sp.A	1B	3	1	1	1			2						
		Daptonema	sp.B	1B	3			1									
		Linhystera	sp.B	1A	4						1						
		Linhystera	sp.C	1A	4	2	1							1		1	
		Manganonema	sp.B	1A	3	3				1	1			1			
		Manganonema	sp.C	1A	3		3			1	2		1		3		
		Manganonema	sp.D	1A	3									1			
		Theristus	sp.A	1B	3											1	
		Theristus?		1B	3			1									
		Xyalidae?		1A	4					1							
		Xyalidae	sp.E	1A	4	2				1							
		Xyalidae	sp.F	1A	4	1											
		Xyalidae	sp.G	1B	4	1											
		Xyalidae	sp.H	1A	4									2			
	LINHOMOEIIDAE	Disconema	sp.A	1A	3											3	
		Paralinhomoeus?		1B	3			1				1	1			1	
	AXONOLAIMIDAE	Ascolaimus	sp.B	1A	3	1			1	5	9	7	10			1	
		Ascolaimus	sp.C	1A	3			1									
	DIPLOPELTIDAE	Campylaimus?		1A	2					1							
		Campylaimus	sp.C	1A	2					1							
		Campylaimus	sp.D	1A	2		2	2					2				
		Diplopeltidae		1A	3					1							
		Diplopeltula	sp.A	1A	3								3	1			
		Diplopeltula?		1A	3				1				1				
		Pararaeolaimus	sp. A	1A	3					1				1			
		Southerniella	sp.A	1B	3				1						1		
		Indet 1		2A	4					1							

Indet 3	1B	3	1	
Indet 4	1A	4		1

Station: 9°N
Whole Core (0-5cm)

Order	Family	Genus	Species	Feeding Group	Tail Shape	BC19 V20 0-1cm	BC19 V20 1-2cm	BC19 V20 2-3cm	BC19 V20 3-5cm	BC20 V16 0-1cm	BC20 V16 1-2cm	BC20 V16 2-3cm	BC20 V16 3-5cm	BC22 V12 0-1cm	BC22 V12 1-2cm	BC22 V12 2-3cm	BC22 V12 3-5cm
ENOPLIDA	THORACOSTOMOPSIDAE	Mesacanthion?		2B	3		1										
	ANOPLOSTOMATIDAE	Anoplostoma?		1B	4		1	2	1				1				2
	PHANODERMATIDAE	Phanodermopsis?		1A	3			2									
		Phanodermatidae?		1A	4			1	1		1						
	IRONIDAE	Doliocholaimus	sp.A	2A	3	1											
		Syringolaimus	sp.B	2A	4										1	1	
		Syringolaimus	sp.C	2A	4				1								1
		Syringolaimus indet		2A	?								1				
		Syringolaimus? indet juv		2A	4	2	60	50	63	1	1	13	21	1	4	9	32
	OXYSTOMINIDAE	Halalaimus	sp.A	1A	4	1	1					2		2	2		1
		Halalaimus	sp.B	1A	4	3	1			1			1				1
		Halalaimus	sp.C	1A	4	2			1	1	1					1	1
		Halalaimus	sp.D	1A	4	1											
		Halalaimus	sp.E	1A	4		2			1				2		1	
		Halalaimus	sp.F	1A	4			1					1	1	2		
		Halalaimus indet		1A	4								1				
		Halalaimus?		1A	4									1			
		Litinium	sp.A	1A	1		1			2	3	1			1	1	1
		Litinium	sp.C	1A	3							1			1		1
		Oxystomina	sp.B	1A	4	1						1					
		Wieseria	sp.A	1A	4							1			1	1	1
	ONCHOLAIMIDAE	Adoncholaimus?		2B	3		1	1									
		Metoncholaimus?		2B	3					1							
		Viscosia	sp.A	2B	3			1				1			1		
		Viscosia?		2B	3						1	1					
CHROMADORIDA	CHROMADORIDAE	Acantholaimus	sp.A	2A	4	6	4		2	4	4	9	4	4	5	3	3
		Acantholaimus	sp.B	2A	4	2		1									2
		Acantholaimus?		2A	4	1								1			
		Actinonema	sp.A	2A	3	1	1				1	1	1		1		
		Chromadora?		2A	3									2			
		Chromadorella?		2A	3		1	1			2	1	2				
		Prochromadorella	sp.A	2A	3	2			1	2	1	1	1	1	1		
	COMESOMATIDAE	Cervonema	sp.A	2A	3			1		1					1	2	1
	ETHMOLAIMIDAE	Nannolaimus?		2A	3							1	1				
	CYATHOLAIMIDAE	Cyatholaimus	sp.A	2A	3		2	2	4	1	1		1				1
		Marylynnia	sp.A	2A	4								1	1			

		Paracanthonchus?		2A	3	1			1			1							
		Paracyatholaimoides?		2A	4	1													
		Paralongicyatholaimus	sp.A	2A	4													1	2
		Pomponema?		2A	4	1													
	DESMODORIDAE	Desmodora	sp.A	2A	3	1						2							
		Desmodora	sp.B	2A	3							1							
		Desmodora	sp.C	2A	3							1						1	
		Paradesmodora	sp.A	2A	3	1							1			1			
	DRACONEMATIDAE	Eudraconema	sp.A	2A	3	1													
	MICROLAIMIDAE	Microlaimus	sp.A	2A	3	6									1	4			
		Microlaimus	sp.B	2A	3							1					1	1	
		Molgolaimus	sp.A	2A	3	2			2	1			1			2	1		
		Nox	sp.A	2A	3							2				1			
		Paramicrolaimus	sp.A	2A	3											1			
	LEPTOLAIMIDAE	Camacolaimus	sp.A	2A	3				I										
		Camacolaimus	sp.B	2A	3	1	2		3				1	1	1			1	1
		Leptolaimus	sp.A	1A	3	3									2		1	1	
		Leptolaimus	sp.B	1A	4	3	2			1		2					1		
		Leptolaimus	sp.C	1A	3	1									1	2			
		Strange Chromadorid		1A	4		2			1				1				1	
	AEGIALOALAIMIDAE	Aegialoalaimus	sp.A	1A	1	1						3		1	1	2	1	1	1
		Cyartonema	sp.A	1A	2										3				1
		Cyartonema?		1A	2							1							
		Diplopeltoides	sp.A	1A	3		1		1			1			1	1	1	1	1
		Diplopeltoides	sp.B	1A	3							3		1				1	1
		Diplopeltoides?		1A	3											1			
		Southernia	sp.A	1A	3											1	1		
	CERAMONEMATIDAE	Pselionema	sp.B	1A	3											1			
	TUBOLAIMOIDAE	Chitwoodia	sp.A	1A	3									2		1	1		
	MEYLIIDAE	Quadricoma	sp.A	1A	3							2				3	1	3	2
		Quadricoma	sp.B	1A	3											1		1	
	DESMOSCOLECIDAE	Desmoscolex	sp.A	1A	3	1				1			1	1			2	2	
		Desmoscolex	sp.B	1A	3	1									1	1	3	1	1
		Desmoscolecidae		1A	3	2						1				4	2	1	
		Amphidless gen nov		1A	3							1	1	1		1	2		
MONHYSTERIDA	MONHYSTERIDAE	Monhysteridae	sp.A	1A	3	2						4				7			
		Monhysteridae	sp.B	1A	4	1						1							
		Monhysteridae	sp.C	1A	4											1			
		Thalssomonhystera	sp.A	1A	4	7	1		1			14		2		4	1		
		Thalssomonhystera	sp.B	1A	4	6	4		5	5		13	4	14	16	3	19	28	16
		Thalassomonhystera	sp.C	1A	3	5	1		1			1	5	3	1	1	13	6	6
		Thalssomonhystera	sp.D	1A	4	5	1		4	6		12	3	13	10	4	7	7	5

	Thalassomonhystera	sp.E	1A	4	1			2			3		1		1	3			
	Thalassomonhystera	sp.F	1A	4	1						2			2	2	3		1	
	Thalassomonhystera	sp.?	1A	4	1														
XYALIDAE	Amphimonhystera	sp.A	1B	4							1			1		2			
	Amphimonhystrella	sp.A	1B	4	1			1	1					1			3		1
	Capsula	sp.A	1B	3										1			1		
	Cobbia	sp.A	2A	4	2		4	2	4		1			1	2	1			4
	Cobbia	sp.B	2A	4												1			
	Cobbia?		2A	4							1					1			
	Daptonema	sp.A	1B	3	1			2					2	1	2				
	Elzalia?	sp.A	1B	2										1					
	Linhystera	sp.A	1A	3				3			2			3	1	5		1	
	Linhystera?		1A	3												2			
	Manganonema	sp.A	1A	3	3		1		1				1	3	3	2	4	2	
	Manganonema	sp.B	1A	3	1		1		3		1			1			1		
	Manganonema?		1A	3	1														
	Paramonhystera?		1B	3	1		1	2						1			1	1	
	Theristus	sp.A	1B	3			1	4	1				1	3	2	2	9		
	Theristus	sp.B	1B	3											5			1	
	Xyalidae?	*sp.A*	2A		1														
	Xyalidae	sp.A	1A								2								
	Xyalidae	sp.B	1A													1			
	Xyalidae	sp.C	1B													1			
	Xyalidae indet																1		
LINHOMOEIIDAE	*Disconema*	*sp.A*	1A	3					2									1	1
	Paralinhomoeus?		1B	3															
	Linhomoeiidae?		1B	3	2											1			
SPHAEROLAIMIDAE	Sphaerolaimus	sp.A	2B	3												1			
AXONOLAIMIDAE	Ascolaimus	sp.A	1A	3	1												1		
	Ascolaimus	*sp.B*	1A	3	1														
DIPLOPELTIDIDAE	Araeolaimus?		1A	3	1														
	Campylaimus	sp.A	1A	2	1								4						
	Campylaimus	sp.B	1A	2				1			1								
	Camplaimus/Diplopeltula		1A	2	1														
	Diplopeltula	*sp.A*	1A	3				2			4				1	3		1	1
	Southerniella	sp.A	1A	3				1								1			
	Diplopeltidae?		1A	3														22	7

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