UNIVERSITY OF SOUTHAMPTON

Abyssal Polychaete Assemblages along Latitudinal Gradients of Productivity in the Equatorial Pacific and North Atlantic Oceans

by

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Signed:

Adrian Glover

Date: 14/04/01

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

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Doctor of Philosophy

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Patterns in polychaete abundance, body size and diversity were investigated at 12 sites between 4300 and 5000 m in the central Pacific and the north-east Atlantic. In the central Pacific, three of the sites (EqPac 0°N, 2°N and 5°N) were observed to lie under high surface productivity regimes, and they were known to receive significant accumulations of food-rich phytodetrital material. The EqPac 9°N, HOT 23°N, DOMES A, ECHO 1 and PRA sites, which did not receive phytodetritus, were used as control sites with which to investigate the effect of this phytodetrital input. In the north Atlantic, one of the sites (PAP) was known to receive phytodetrital input, and one of the sites (MAP) had been subjected to a large-scale natural disturbance in the form of a turbidite emplacement.

All specimens were identified to species level. Two families, the Pilargidae and Cirratulidae were selected for a more detailed alpha taxonomy assessment. New characters were developed for the identification of cirratulid thoracic fragments.

Benthic polychaete abundance was correlated with surface productivity in both the Pacific and Atlantic Oceans. There was some evidence to suggest that there was a stronger benthic-pelagic link in the Pacific Ocean, where small changes in surface productivity generated larger changes in abundance than in the Atlantic Ocean. When data from previous studies are included, it is suggested that at levels of surface productivity above 200 $gCm^{-2}yr^{-1}$, there is an upper limit to benthic polychaete abundance.

Significant differences in body size between sites were found at species level, family level and for the entire polychaete taxon. At a species level, several abundant cosmopolitan deposit feeding species showed reduced body size in the food-rich phytodetrital sites. The only species to show increased body size in the food-rich sites were two predatory species. Polychaetes in the Atlantic Ocean responded more strongly in terms of body size reduction in phytodetrital sites than they did in the EqPac sites. Three hypotheses were put forward to explain these patterns: increased metabolic efficiency of large organisms in food-poor regions, seasonal recruitment pulses at phytodetrital sites and increased competition at phytodetrital sites. The former was favoured as the most likely explanation.

Species diversity was shown to be highest in the phytodetrital sites in the central Pacific. It was hypothesised that this was the result of increased productivity, increased spatio-temporal heterogeneity and increased sediment heterogeneity at these sites. An increase in species diversity at phytodetrital Atlantic sites was not observed. The differences between north Atlantic and central Pacific sites were attributed to regional enrichment of local diversity in the Pacific.

At the MAP turbidite site, alpha diversity was significantly lower than at other sites, and dominance was high, indicating the potential for large-scale natural disturbance in the abyss. A new spatio-temporal scale of disturbance was highlighted that may have evolutionary as well as ecological significance.

Although levels of alpha diversity were generally shown to be high in the abyss compared to shallow water, the evidence did not suggest in favour of high beta diversity on scales of 1000 to 3000 km in either the central Pacific or north Atlantic. The low levels of beta diversity observed suggest that total species richness in the deep sea may not be as high as previously hypothesised, and that regional processes are likely to significantly impact local ecology in the deep-sea.

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I would like to dedicate this thesis to my mother, Emily.

1 INTRODUCTION

1.1 The Historical Context

Until the mid 19th century, the great depths of the ocean were regarded as a remote and lifeless zone. Edward Forbes, a young professor of Zoology at Edinburgh University in the 1840s helped push the scientific community into sampling this vast region. Although highly influential in originating the science of oceanography, he is unfortunately best remembered for suggesting that the deep sea was likely to be lifeless below 520m, based on some observations he had made whilst dredging in the Aegean Sea (Forbes, 1844; Forbes, 1856). Even so, these early ideas stimulated discussion, and prompted many to sample the depths to test Forbes' theory. Wallich (1860) found ophiuroids at 2300m and serpulid polychaetes from 1250m. The Norwegian naturalist and minister, Michael Sars (1865) listed several invertebrates from sites at 600m off the Lofoten Islands. Pourtales (1867) discovered invertebrates from 938m for the US Coastal Survey, and Malmgren (1870) recovered benthic fauna from 1400m off Spitzbergen. These discoveries led to the Royal Society dredging expeditions on HMS *Lightning* and HMS *Porcupine* in 1869 and 1870. These early cruises recovered material from the Rockall Trough and off the Iberian Peninsula down to depths of 4300m, and demonstrated finally the presence of life in the deep areas of the ocean. These expeditions were led by the Edinburgh professor Charles Wyville Thomson (Thomson, 1874), and he was also instrumental in setting up the much more ambitious HMS *Challenger* expedition of 1872 – 1876. The *Challenger* was the first multi-disciplinary oceanographic cruise around the world and provided a quantum leap for the science of oceanography. Amongst its many achievements were the first systematic plot of currents, temperatures and depths for the world oceans, generating maps of the types of bottom deposits and the description of 5000 new species of marine life.

HMS *Challenger* began the period of the great pioneering oceanographic expeditions, each named after the ship that carried them – the US steamers *Blake* (1877-96) and *Albatross* (1887-1925), the Danish *Ingolf* Expedition (1896-98), the Deutsche Tiefsee Expedition aboard the *Valdavia* (1898) and later, the Swedish *Albatross* (1947-48) and Danish *Galathea* expedition (1950-52). All of these expeditions made significant contributions to the growing science of oceanography, yet it was not until the 1960's that the next major deep-sea discovery took place. Eschewing the search for the larger creatures of the deep, Robert Hessler and Howard Sanders of the Wood's Hole Oceanographic Institution focussed their efforts on the smaller organisms down to just 500 microns in length. Most previous studies had used deep-sea nets with mesh sizes of several millimetres, as is common in shallow-water methods. The results were surprising; both infaunal and epifaunal organisms were highly speciose, far more so than had been previously hypothesised. This formed the basis of their seminal work 'Faunal diversity in the deep-sea' (Hessler and Sanders, 1967), still one of the most cited papers in biological oceanography today. Scientists continue to discuss the central paradox of this paper – how can such a quiescent and food impoverished habitat rival a coral reef or rainforest for species richness?

Sanders' (1968) comparative study of marine benthic diversity was the first to address this question. Using data from a variety of marine habitats collected using similar methodologies he demonstrated that the species diversity was higher at tropical and deep-sea sites and lower at equivalent boreal and shallow water habitats. He postulated that this was the consequence of the greater physical stability of these habitats over time and of 'biological accommodation' of species. The constancy of the deep-sea environment insulates the species from the physical alternations above whilst permitting gradual speciation and niche differentiation over a great length of time- the *stability-time* hypothesis.

The stability-time hypothesis was evolutionary in its scale; while it explained why there might have been so much potential speciation in the deep sea it did not explain how it was that so many species could coexist on an ecological scale. Dayton and Hessler (1972) followed this argument when they proposed that disturbance in the form of 'predatory cropping' is important in permitting species coexistence. In this hypothesis, all deep-sea benthic species are food generalists, consuming anything smaller than themselves. Small species that are constantly 'cropped' by larger species may well be predator-limited while the larger species are more likely to be food limited. This argument was countered by Grassle and Sanders (1973), who showed that the life-history characteristics of deep-sea animals (i.e. low reproductive and growth rates) did not support the idea that they were subject to high levels of predation. They suggested instead that diversity may be enhanced both by niche diversification and the presence of a temporal mosaic of micro-succesional stages, an early version of the more modern *patch-dynamic* model.

Abele and Walters' (1979) critique of Sanders (1968) highlighted the potential pitfalls of comparative studies, although they agreed with Sanders in stressing the importance of evolutionary explanations for diversity. They demonstrated that the areal extent of the habitat being investigated may account for up to 99% of the variation in polychaete species numbers. Three possible explanations for the species-area relationship were invoked in this case; (1) reduced extinction rates in larger habitats; (2) increased habitat heterogeneity and (3) a sampling phenomenon. This argument was the precursor to more recent papers (Ricklefs, 1987; Cornell, 1993) that explore the influence of regional diversity on local diversity. Large habitats such as the deep sea have a greater potential species pool, or high 'regional' diversity. Local diversity is a product of both the regional species pool and fine-tuning by local ecological processes such as disturbance. The point was, in comparative studies of diversity it is essential to be precise in determining the scale of diversity being measured.

In the mid 1970's a considerable methodological advance was made with the introduction of the USNEL spade box corer (Hessler and Jumars, 1974). This device (see section 3.1.3) permitted virtually undisturbed 0.25 m^2 cores of sediment to be taken from both bathyal and abyssal depths. Hessler and Jumars' 1974 paper was the first fully quantitative study of the very deep oligotrophic abyssal sites which were previously thought to be impoverished. Using ten box cores from the CLIMAX II site at 5500 m they showed that of the mean 115 individuals per m^2, 55% were polychaetes and that species diversity as measured by rarefaction was higher than anything reported by Hessler and Sanders on the Gay Head-Bermuda transect. The majority of the polychaete species were deposit-feeding food generalists of the family Cirratulidae.

This discovery of high local scale diversity in such an oligotrophic habitat stimulated further research into the relationship between productivity and diversity in the marine system. In terrestrial systems, this relationship has been intensively investigated (Rosenzweig and Abramsky, 1993; Rosenzweig, 1995; Gaston, 2000). Oceanic surface-water productivity was known to vary on both spatial and temporal scales, but it was not known how insulated the deep sea was from these variables.

A considerable advance was made in this respect by sedimentary geologists in the early 1980's. Deuser and Ross (1980) used moored sediment traps in the Sargasso Sea to show that variations in the flux of organic carbon to the sea bed were related to changes in surface productivity. Billett *et al.* (1983) used a time-lapse photography system to record the seasonal deposition of phytoplankton following the spring bloom in the euphotic zone of the Porcupine Seabight. Photographs showed the rapid accumulation of well preserved phytoplankton remains, principally diatoms, that were directly related to the flora of the spring bloom above.

The discovery of seasonality on the abyssal sea floor was significant in changing the paradigm of the stable, quiescent deep sea; further evidence for this was available from research into the physical environment (Gage and Tyler, 1991). Sedimentary perturbations such as slips, slumps and the more violent turbidity currents can have a dramatic effect on benthic fauna, possibly causing large scale extinctions (Aller, 1989). On a smaller scale, changes in the energy of the benthic boundary layer can cause sediment resuspension and disturbance. Thistle *et al.* (1985) reported that at the High Energy Benthic Boundary Layer (HEBBLE) site, macrofaunal abundance was considerably enhanced relative to other sites of comparable depth, indicating the importance of current dynamics in the resuspension of food particles.

The realisation that the deep sea was not the tranquil environment inherent in Sanders' stability-time hypothesis led to a re-evaluation of diversity theory. Parallel studies on land during the late 1970's overturned the notion that diverse communities are the result of equilibrium processes and ordered succession. Connell (1978) developed the intermediate disturbance hypothesis to explain diversity in tropical forests and coral reefs. The classic bell shaped curve describes how diversity is maximised when either disturbance frequency or predator intensity is at an intermediate level. Huston's (1979) model combined both frequency of reduction (disturbance and predation) with rates of competitive displacement (related to productivity) predicting that diversity would be highest when both are at an intermediate level. He used the evidence for a bathymetric gradient of diversity along Hessler and Sanders' Gay Head-Bermuda transect as evidence to support his model. Further evidence for the bathymetric gradient came from analysis of gastropod molluscs (Rex, 1973; Rex, 1976; Rex, 1981) and polychaetes (Paterson, 1993; Paterson and Lambshead, 1995).

By the mid 1980's, scientists views of the deep sea had radically altered. In just twenty years, the notion of a stable, faunally impoverished deep-sea benthos had been replaced by the idea of a highly diverse, dynamic system, fluctuating over both spatial and temporal scales. Hessler and Jumars' (1974) discovery of such high diversity on a local scale spurred researchers to make experimental investigations of the processes involved. Grassle and Sanders suggested in their 1973 paper the importance of a temporal mosaic of species successions; Smith *et al.* (1986) and Grassle and Morse-Porteous (1987) further developed the idea of *patch dynamics* by using an experimental approach. Using the submersible 'Alvin' they placed trays of azoic sediment and patches of organic material onto the sea bed. The colonisation by opportunistic polychaetes of the organic additions suggested to them the importance of (1) patchiness of organic input; (2) sporadic small-scale disturbance and (3) the lack of barriers to dispersal in the 'open' marine system. These ideas were supported by the experimental work of Levin and Smith (1984) and Desbruyères *et al.* (1985). This patch dynamic model stressed the importance of an ephemeral food source and the variability in life-history characteristics in deep-sea organisms, something that had not been fully appreciated before.

Researchers began to realise that similar processes may be maintaining diversity in the deep sea as in the highly speciose tropical forests and coral reefs that had been much more intensively studied. This led to some scientists questioning whether marine benthic diversity may rival that found in other ecosystems. Grassle and Maciolek (1992) in their intensive study of macrofaunal samples from the continental slope and rise suggested that there may be up to 10^7 species owing to the great area of the oceans and the rapid increase in species number as samples are added together. This proposition generated considerable debate; Briggs (1991) had already highlighted the problems of extrapolation from limited data, while May (1992) argued that species replacement along a gradient is not linear, but rather because half the species they collected were already known to science then the total number of species is unlikely to be more than half a million (twice the number currently described). Poore and Wilson (1993) countered by implying that Grassle and Maciolek may have actually underestimated species richness at both slope and abyssal depths for the isopod fauna. Lambshead (1993) suggested that there may be ten million nematode species in the deep sea, although clearly stated the difficult of making such extrapolations.

The discussions of species number led on to discussions of global diversity patterns. Spatial variation in diversity on a global to regional scale has taxed the minds of terrestrial ecologists for a long time. It is universally agreed that many more species are present in the tropics than in temperate latitudes and several reasons have been put forward to explain this, reviewed by Rohde (1992). Some suggest that it is primarily an area effect (Rosenzweig, 1995) whilst others argue that it is the combination of many influences, such as time, species ranges and productivity (Rohde, 1997).

Rex *et al.* (1993) suggested that there was a latitudinal decline in deep-sea species from the tropics to the Arctic, invoking regional explanations for a regional pattern. For example, they suggested that reduced diversity in the Norwegian Sea was the result of the Quaternary glaciation and the build up of sea ice. Rex *et al.* (1993) was criticised on methodological grounds by May (1992), Gage and May (1993) and Gray (1994) who all pointed out that rarefaction, as it is affected by the relative abundance of species (or equitability), was not a suitable measure of regional species richness (i.e. the number of species). Rex *et al.* (2000) countered this by showing how their rarefaction values correlated well with other measures of species diversity such as species number and evenness. However, Lambshead *et al.* (2000) have shown how that there is no clear latitudinal gradient for nematodes and if anything, there is an increase in nematode diversity with latitude in the north Atlantic. Similarly, Glover *et al.* (2001) indicated that for polychaetes, there was no relationship with latitude when rarefaction methods were used, and that when species number only was measured, there was a slight increase in diversity with increasing latitude.

This brief history can be summarised as follows; the first 100 years of deep-sea research, from the *Challenger* expedition to Hessler and Sanders' work were a period of discovery and taxonomy. Since the late 60's there has been more emphasis on the quantitative aspects of diversity and the processes behind it. In the last few years, the emphasis has shifted again, with many researches focussing on the biodiversity of the deep-sea benthos and the biogeochemical processes affecting it. In Chapter 2, the relevant theoretical framework and hypotheses to be tested are outlined in more detail.

1.2 Polychaetes

Polychaetes are a very diverse class of annelid worms closely allied to the earthworms and leaches (the Clitellata). Rouse and Fauchald (1997) considered the polychaetes a monophyletic group based on the presence of nuchal organs, ciliated sensory structures just behind the prostomium. Nevertheless, it seems probable that future revisions may cast doubt on the monophyly of the group; certainly the former 'phyla' Pogonophora and Vestimentifera must now be considered as a family among the polychaetes (Rouse and Fauchald, 1997; Kojima, 1998). Paleozoic polychaete fossils are present from the Cambrian and Ordovician. The major differentiation of these Paleozoic polychaetes suggests that most of the major family clades had already appeared before the break up of Pangaea at the end of the Permian. The great age of these clades precludes biogeographic patterns at the family level, at least those present as a result of phylogenetic history, as the polychaetes could have got everywhere by simply drifting around on the continents (Fauchald, 1984).

Polychaetes are not well represented in the fossil record and the time of radiation into the deep sea is not known. Major extinctions in the deep sea caused by anoxia during the Mesozoic and start of the Palaeocene (65 - 56 mya) suggest that the modern deep-sea fauna originates from after this time, with species re-invading from bathyal refugia (Lipps and Hickman, 1982; Rogers, 2000). There are few exclusively deep-sea families, and most genera have shallow-water counterparts, supporting this 'recent fauna' hypothesis. Nevertheless, the polychaetes are extremely diverse at a species level in the deep sea (Figure 1.1), and constitute some 60-70% of the macrofaunal organisms by abundance (e.g. Grassle and Maciolek, 1992).

Hartman and Fauchald (1971) wrote:

> *'The single most conspicuous feature of the abyssal polychaetes... is the uniformly small size and the reduced number of body segments at maturity, as compared with their shallow water relatives'*

This reduction in body size is one of the main adaptations of the deep-sea fauna. Yet there has been limited specialisation of deep-sea polychaetes; nearly all abyssal genera have shallow-water representatives. It may well be that the great diversity of polychaetes in the deep sea is not a result of invasion and subsequent radiation, rather it is the result of invasion of already highly radiated shallow water forms, coupled with the great areal extent of the abyssal plains. This is in contrast to the pattern for the Asellota (Isopoda), which appear to have undergone a much longer period of evolution and speciation in the deep sea, and perhaps survived through the Mesozoic extinction periods (Wilson, 1999).

In this study, polychaetes are the study taxon selected to address a series of ecological questions. A justification is needed for the study of one taxon when the questions may pertain to the whole community. The justification is as follows: (1) a 'total community' approach is not pragmatic given the difficulties of applying taxonomic expertise to a wide ranch of taxa within a limited time-frame, this is especially true at this time when there are more demands than ever on fewer and fewer taxonomists; (2) the total community approach may obscure ecological responses to environmental variables – this may happen when taxa from a variety of different

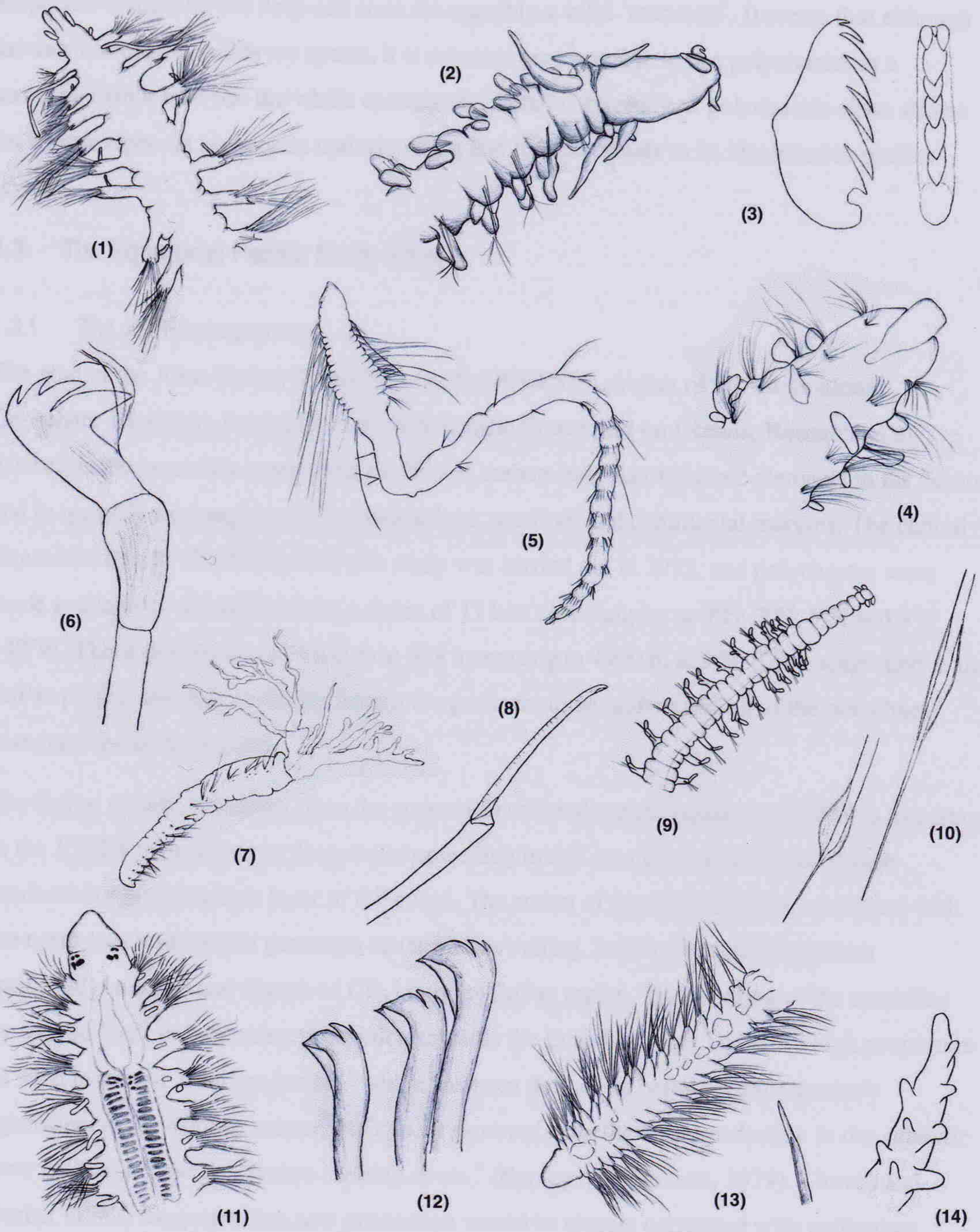

Figure 1.1 Polychaete morphological diversity in the abyss. Polychaete morphologies from the central equatorial Pacific and Madeira Abyssal Plain, north-east Atlantic: (1) *Brania* sp. 867 (Syllidae), (2) *Pseudomystides limbata punctata* sp. 798 (Phyllodocidae), (3) Thoracic uncini of Ampharetidae sp. 915, (4) Spionidae sp. 612, (5) *Chaetozone* sp. 828 (Cirratulidae), (6) Thoracic chaetae of Maldanidae sp. 938, (7) *Jasmineira* sp. 919 (Sabellidae), (8) Compound chaetae of *Flabelligella* sp. 860 (Acrocirridae), (9) *Progoniada regularis* (Goniadidae), (10) Thoracic palaea of Sabellidae sp. 920, (11) *Exogone* sp. 873 (Syllidae), (12) Abdominal hooks of *Spiophanes* sp. 885 (Spionidae), (13) Orbiniidae sp. 845, (14) Papillated dorsal cirrus of *Ancistrosyllis* sp. 835 (Pilargidae)

spatial scales are included in the same analysis – tiny sediment-dwelling nematodes, for example may respond to a completely different set of parameters to large, mobile surface grazing holothurians; (3) the 'taxocene' approach of Hurlbert (1971) advocates the analysis of one grouping of organisms that respond to environmental variables in the same way; and (4) polychaetes, occupying a similar size range with limited mobility and being, in general, unspecific feeders on the deep-sea ooze are arguably a valid 'taxocene'. It seems that although the data on feeding guilds are sparse, it is no more unreasonable to use polychaetes as a taxocene than it is to use the whole community. Finally, the study of polychaetes alone allows for a more rigorous taxonomic understanding and for individuals to be identified to species level.

1.3 The Equatorial Pacific Study Sites

1.3.1 The JGOFS programme

The goal of the Joint Global Ocean Flux Study (JGOFS), a project of the International Geosphere-Biosphere Programme of the Scientific Committee on Oceanic Research is to determine the processes controlling the flux of carbon and other biogenic elements in the oceans and to quantify exchanges with the atmosphere, sea floor and continental margins. The central Equatorial Pacific (EqPac) part of this study was carried out in 1992, and polychaetes were made available to the author from a series of 17 box core samples at 0°N, 2°N, 5°N and 9°N 140°W. The water depth was 4300 m at 0°N increasing to 4900 m at 9°N. The background to the EqPac project and data available from it are pertinent to an understanding of the polychaete communities at the sea bed.

The EqPac region, stretching from the coast of Ecuador along the equator to 170°W is important to the JGOFS programme as deep-water upwelling in this area generates a band of high productivity in the surface layer of the ocean. The action of the Coriolis force, combined with the north-east trade winds generates equatorial upwelling, feeding inorganic nutrients (principally nitrates and dissolved CO_2) into the EqPac region. The shoaling of the nutricline eastbound leads to increasing production towards the Ecuador coast. There is a high proportion of what is termed 'new production' which has been defined as being "*...quantitatively equivalent to the organic matter that can be exported from the total production in the euphotic zone without production system running down.*" (Eppley and Peterson, 1979). Chavez and Barber (1987) suggested that new production would be closely correlated with particulate organic carbon (POC) flux to the sea bed. One of the major goals of the EqPac programme was to investigate and quantify the fate of this exported organic carbon.

The significance of the EqPac region is that it may account for 25-50% (0.9 gigatons) of global ocean production (Chavez and Barber, 1987; Barber *et al.*, 1994). The EqPac region was also of interest to the JGOFS scientists for three further reasons: (1) interannual variations in ocean-atmosphere fluxes associated with the El Niño Southern Oscillation (ENSO) events indicate a short-term connection between climate change and CO_2 flux, (2) the sediments beneath the upwelling zone contain large amounts of organic carbon and hence may contain a record of past climate changes on a larger scale and (3) the area is an example of a high nutrient, low chlorophyll (HNLC) regime – or, the levels of production are not as high as predicted by computer models based on inorganic nutrient (principally dissolved CO_2 and nitrate) availability (Murray *et al.*, 1992; Murray *et al.*, 1994). This final point has in part been answered by the EqPac study, and it appears that the main limiting factors on productivity are iron limitation and grazing pressure (Murray *et al.*, 1997).

The 1992 EqPac programme occurred during an El Niño event. El Niño is an anomaly in the normal ocean-atmosphere interaction system in the central Pacific (Philander, 1989). In a normal year, trade winds formed by the action of insolation and the Coriolis effect blow westward across the central Pacific, pushing the warm surface waters towards Indonesia; sea surface height is normally about 1/2 m higher off the coast of south-east Asia than off the coast of Peru. The westward movement of surface water reduces the depth of the thermocline in the east Pacific region, and productivity is enhanced off the coast of Peru by this upwelling of cool, nutrient-rich deep water. Depending on the strength of the cooling, productivity may be enhanced in the equatorial surface waters as far as 170°W, as the prevailing westerlies continue forcing the surface waters towards Asia. It is this general circulation model that is the primary cause of the high productivity of the EqPac region.

El Niño is marked by a change in this circulation model. It both causes, and is caused by, a weakening in the prevailing westerly trade winds. The weakening of the trade winds is known as a Southern Oscillation, marked by a reduction in the barometric pressure differential between Tahiti and Darwin. The precise 'trigger' of El Niño is not understood, only that once it has started, feedback systems amplify it. The weakening of the trade winds results in reduced movement of surface water westward, and hence reduced upwelling off nutrient-rich cool waters off the Peruvian coast. The term El Niño was coined by Peruvian fishermen to describe this warming in surface waters off the coast of Peru, associated with a decline in fish stocks around Christmas time. El Niño may affect many climatic and oceanic variables, but the one pertinent to this study is the reduction in surface productivity across the central equatorial Pacific region from the Peruvian coast to 170°W. In most El Niño years, the sea-surface temperature (SST) warming starts in November-December and continues for approximately six months, at which point the situation usually reverses generating cool SST's and what is sometimes referred to as a La Niña period. Productivity during a La Niña period is enhanced along the equatorial Pacific, as the normal circulation model is returned, only more strongly than normal. Recently, there have been strong El Niño's in 1982, 1987, early 1992 and 1997/98 and La Niña's in 1987, 1998 and 1999. These data are freely available from the NOAA's Climate Prediction Centre internet site[1].

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[1] http://www.cpc.ncep.noaa.gov

In 1992, El Niño continued only until July, whereupon the trade winds started to strengthen and there was a cooling of SST's (Barber *et al.*, 1994). By August, the cool tongue of nutrient rich water had returned to the EqPac region and productivity had increased.

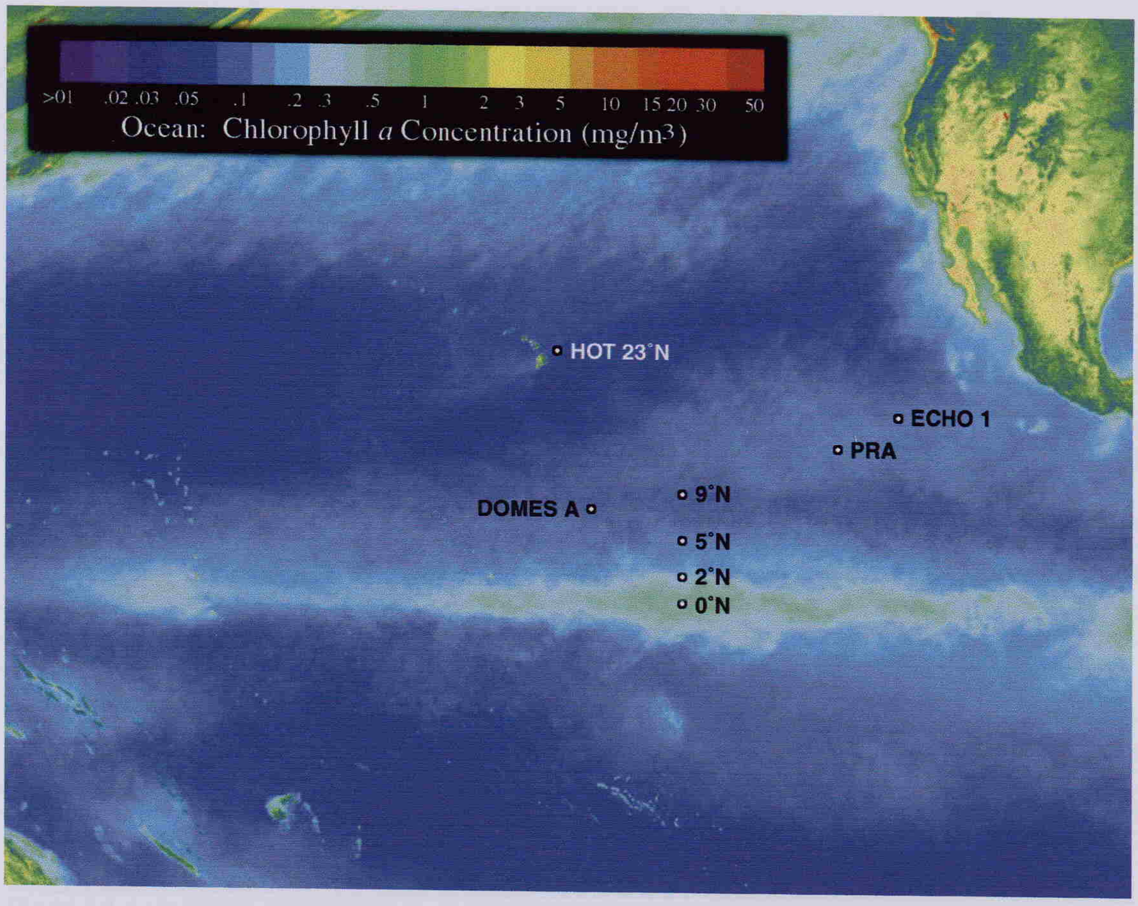

Figure 1.2 SeaWIFS satellite based chlorophyll concentration data for the central equatorial Pacific during a La Niña 'cool' period, showing the strong latitudinal gradient of productivity over the equator. Positions of EqPac, HOT, DOMES A, ECHO 1 and PRA sites are shown. Note that these measurements were taken during August 1998 – i.e. not during the period of study (1992) when there were no satellite data available. August 1998 is representative of a cool period similar to that which occurred during the latter half of 1992.

Box-core samples for this study were collected in November 1992 immediately following this cool period. The satellite based chlorophyll measurements show how cooling of the surface waters and associated upwelling of deep nutrients generates the band of high productivity along the equator (Figure 1.2). One question that is pertinent is the degree to which the 1992 cool period was stronger than under normal circulation models – i.e. whether productivity was likely to have been enhanced in the months prior to box core sampling. It is unfortunate for the EqPac study that there was no overflying satellite available during the study; the data for Figures 1.2 and 1.3 comes from the SeaWIFS satellite which was not launched until 1997 (the effects of the El Niño and La Niña events of 1997-98 are shown). Its predecessor, the CZCS satellite was discontinued in 1986. However, there is some evidence to suggest that the August – October 1992 period was especially productive (Barber *et al.*, 1994). Primary productivity during this period was 75% higher than the climatology mean for 1987-1991. Against this observation it must be stated that the climatology mean is affected by the warm, low production periods and that the inorganic nutrient levels for August – October were no higher than normal.

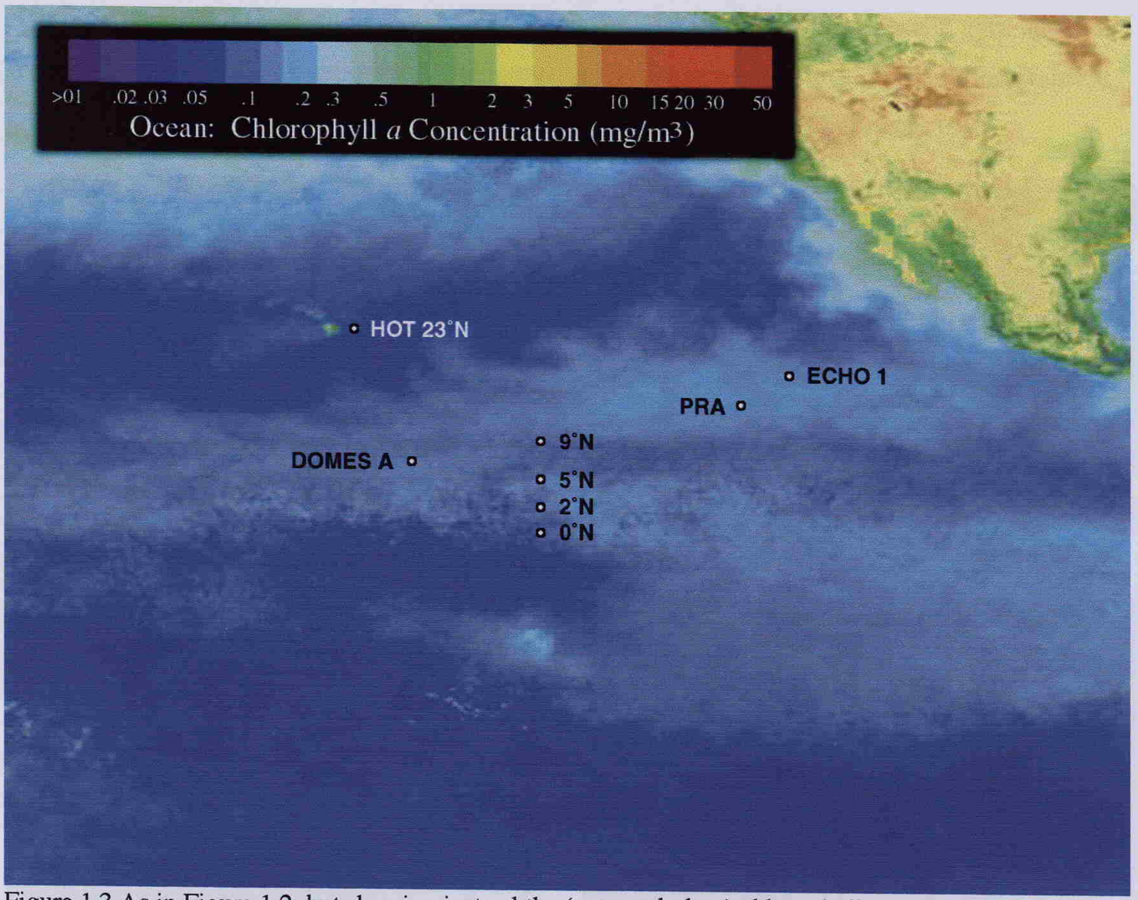

Figure 1.3 As in Figure 1.2, but showing instead the (extremely low) chlorophyll concentrations during an El Niño 'warm' period, in this case, mid-1997. Note that the map projection is slightly different to that in Figure 1.2.

The export production of organic carbon and associated biogenic elements has been explored by Honjo *et al.* (1995) and the fate of the particulate matter at the sea bed by Smith *et al.* (1996, 1997). Honjo *et al.* deployed a series of moored sediment traps along the 140°W transect at water depths of approximately 1200m, 2200m and 700m above the bottom. Particulate organic carbon flux in the region of 300-370 μmol m^{-2} day^{-1} was recorded for the 0° N to 5° N decreasing to just 80 μmol m^{-2} day^{-1} at the 9° N site. Smith *et al.* (1996) recorded the presence of fresh phytoplankton detritus (or phytodetritus) at the 0°N, 2°N and 5°N sites but not at 9°N (Figure 1.4), and concluded that it was an important food source for the benthic microbes and metazoans. Smith *et al.* (1997) demonstrated that rates of bioturbation were significantly enhanced at the phytodetrital sites (0°N, 2°N and 5°N) and suggested that macrofaunal abundance in particular may be the best correlate with particulate organic carbon flux. These results, the presence of phytodetritus and the enhanced productivity at the equatorial sites are discussed further in the relevant chapters 5 and 6. Uniquely, the EqPac transect allows an examination of polychaete abundance and diversity patterns alongside a wealth of supplementary oceanographic data.

A series of box cores from the Hawaii Ocean Time Series (HOT) station at 23°N 158°W have also been examined (Karl and Lukas, 1996). This site, lying in the central Pacific gyre under a regime of year round low productivity (Figure 1.2) has been used alongside the EqPac transect sites as a control site. The collections were made in August 1992 and February 1993.

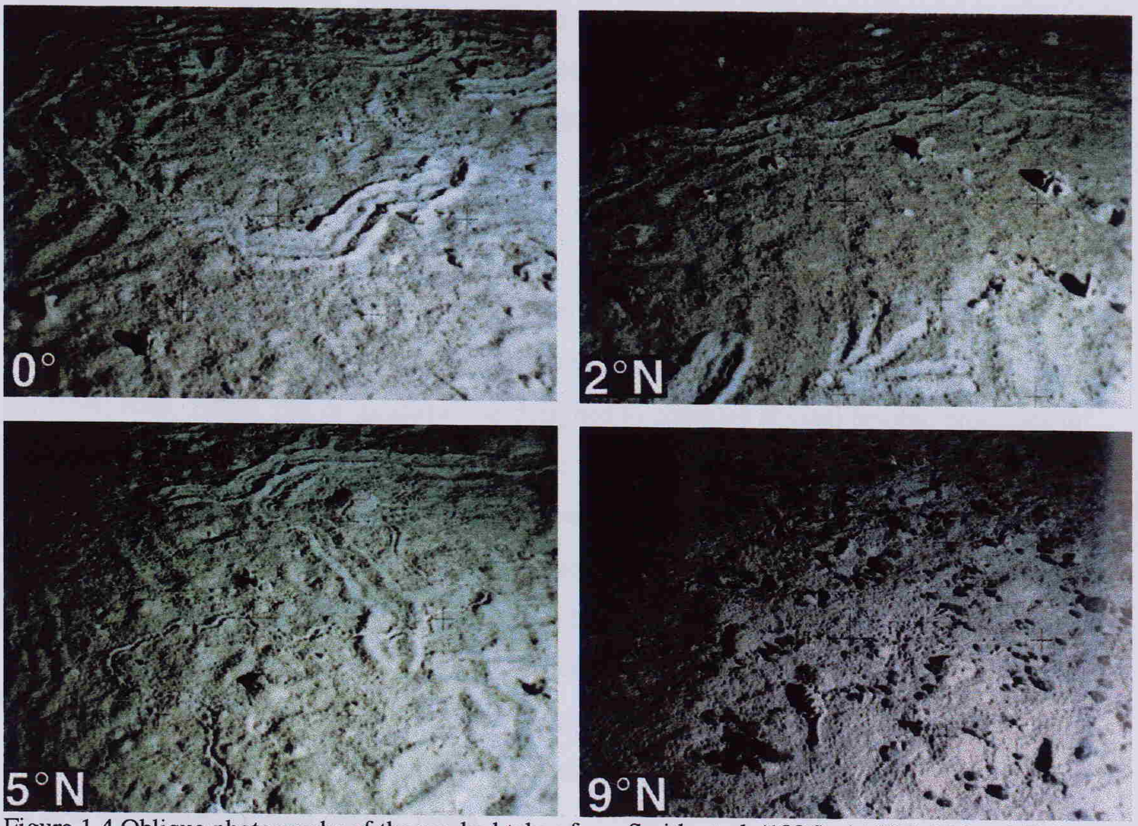

Figure 1.4 Oblique photographs of the sea-bed taken from Smith *et al.* (1996). At 0°N, 2°N and 5°N greenish phytodetrital material is present, this is absent from 9°N where steady-state sedimentary dynamics have led to the accumulation of manganese nodules (dark patches). At the phytodetrital 0°N, 2°N and 5°N, there are abundant traces of megabenthic grazers, these are absent at 9°N.

1.3.2 The manganese nodule provinces

The manganese nodule area is located at approximately 4500 m depth, east of the EqPac transect and bordered by the Clarion - Clipperton fracture zones and the East Pacific Rise. The area has been intensively studied as part of the Deep Ocean Mining Environmental Study (DOMES) (Piper and Blueford, 1982), the ECHO 1 expedition (Wilson and Hessler, 1987) and the Preservational Reserve Area (PRA) study (Wilson, 1990; Wilson, 1992). Data are made available for analysis in this thesis[2] from DOMES site A (8°27'N 150°47'W), ECHO 1 (14°40'N 126°25'W) and PRA sites (12°57'N 128°19'W). The samples were collected as part of a study of the effects of trial mining for manganese nodules by Ocean Mining Associates (OMA). No differences in community structure or diversity could be found between test sites

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[2] I am grateful to Dr G.D.F. Wilson of the Australian Museum, Sydney for providing me with data from these sites.

and undisturbed control sites, although the authors pointed out that this may be the result of under-sampling of the communities (Wilson and Hessler, 1987). Nevertheless, in terms of the number of samples, these are some of the most intensively studied abyssal habitats to date.

These data have been used here for comparison with the highly productive EqPac sites. In terms of productivity, the manganese nodule sites lie under a similar regime to the 9°N EqPac site. Comparing high productivity sites with low productivity sites is difficult as there are likely to be great differences in the number of individuals. In other words, many more samples are needed from the low productivity sites for meaningful comparisons to be made. 15 box core samples were taken from ECHO and PRA, and 47 from DOMES A. The position of the sites is indicated in Figures 1.2 and 1.3.

1.4 The North Atlantic Study Sites

Contrasting abyssal sites in the north Atlantic were studied as part of a European Union Marine Science and Technology (MAST) collaborative research programme in the early 1990's (Rice *et al.*, 1994; Rice, 1995). The programme was designed to compare abyssal benthic processes in the northerly Porcupine Abyssal Plain (PAP) site with those at more southerly sites on the Tagus Abyssal Plain (TAP), Madeira Abyssal Plain (MAP) and Cape Verde Abyssal Plain (EUMELI oligotrophic site, EOS). These sites had already been sampled in an earlier MAST programme (Rice, 1993) that had shown there to be significant differences in the nature and amount of organic input, the degree of disturbance and the spatial variability of benthic fauna. The PAP site had also been sampled as part of the IOSDL DEEPSEAS programme (Rice *et al.*, 1994) that tested hypotheses concerning the effect of a seasonal deposition of phytodetritus at the PAP site on the abyssal benthic fauna.

The PAP site, is centered on 48°50' N 16°30' W in 4850 m of water (Figure 1.5). With a winter mixed layer in excess of 500m the area has been shown to receive a strong seasonal pulse of macroscopic phytodetritus to the sea bed (Figure 1.6) (Rice *et al.*, 1994). The PAP site lies 150 nautical miles northeast of the German BIOTRANS site , and was originally selected for its relatively simple bottom topography. 5 box core samples were studied at this site.

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[2] I am grateful to Dr G.D.F. Wilson of the Australian Museum, Sydney for providing me with data from these sites.

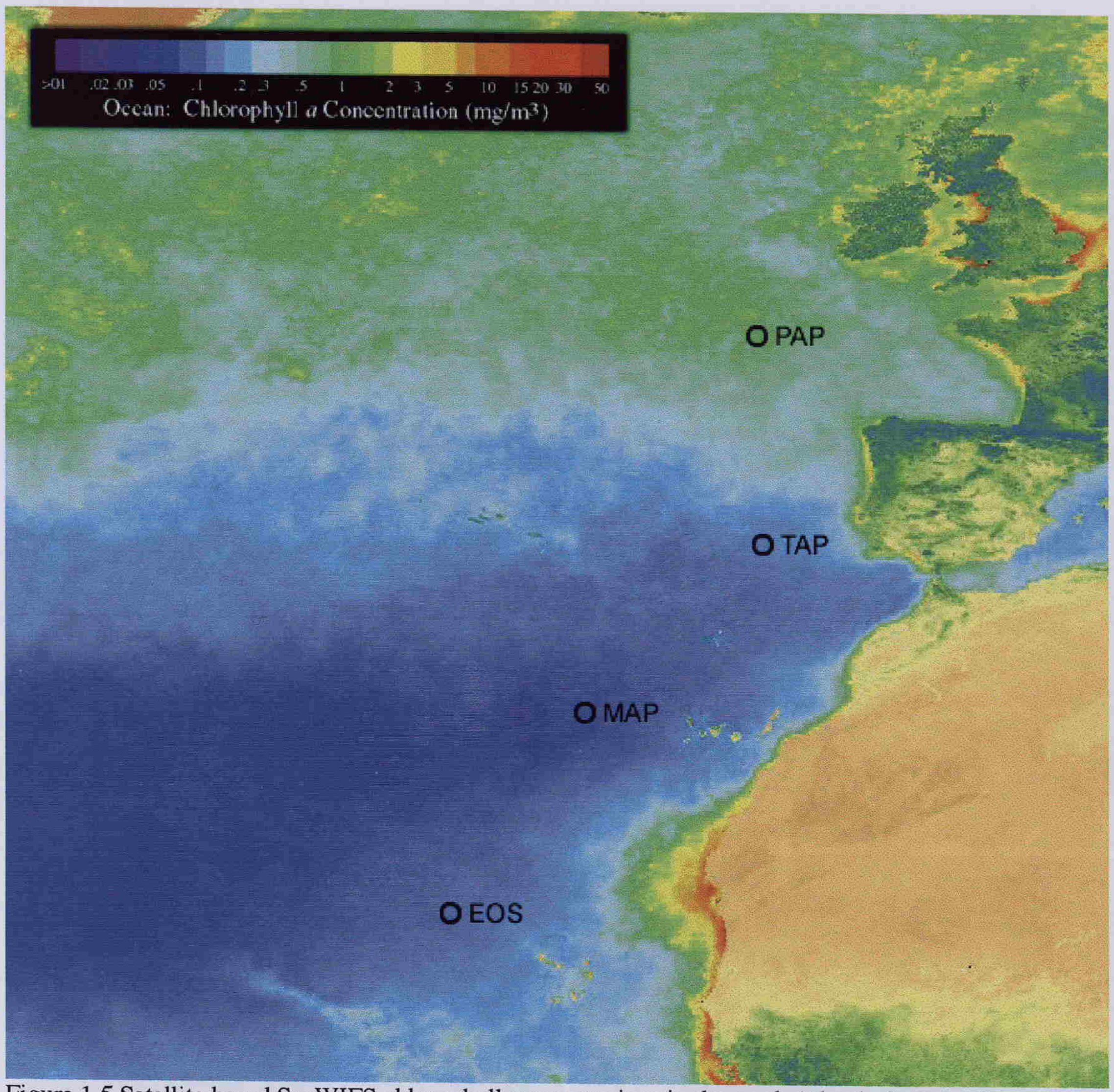

Figure 1.5 Satellite based SeaWIFS chlorophyll concentrations in the north Atlantic for June-August 1998, Showing the locations of the four north Atlantic sampling sites.

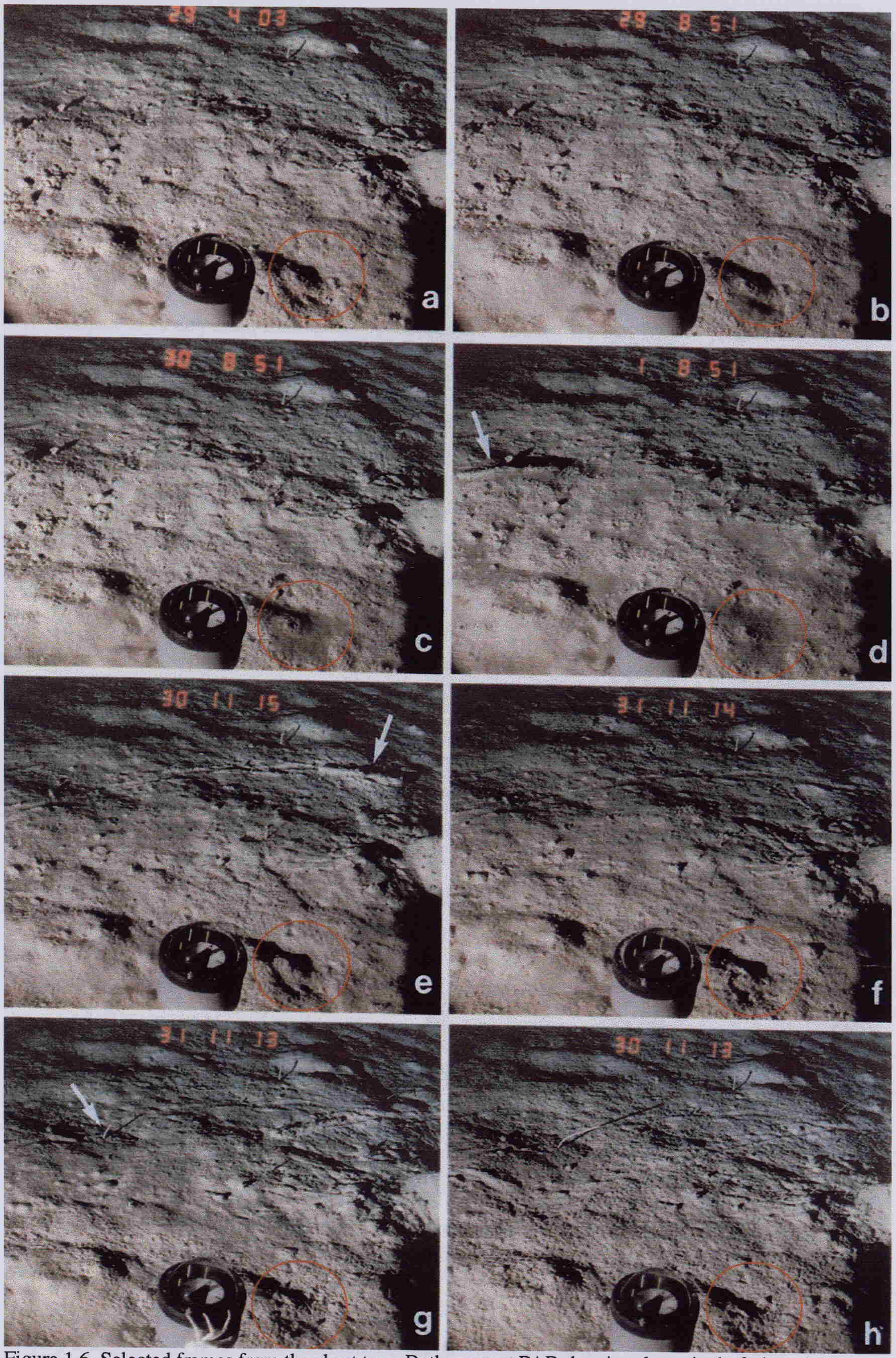

Figure 1.6 Selected frames from the short term Bathysnap at PAP showing the arrival of phytodetritus at the sea bed. In, (a), May 1991 no phytodetritus evident, (b) showing first arrival of phytodetritus (red circle) 29 May, (c) some additional phytodetritus (red circle), (d) abundant phytodetritus (red circle) and pseudostichopod holothurian (arrowed) 1 June, (e) reduced phytodetritus 30 June, (f) phytodetritus hardly visible 31 August, (g) phytodetritus possibly still discernable, and new worm tube (arrowed), (h) no evidence of phytodetritus, worm tube much larger (taken from Rice *et al.* (1994))

The TAP site is centered on 38°N 11°W at 5035 m depth. The area is thought to be physically quiescent, with abundant biogenic traces, indicative of low current flow (Gage *et al.*, 1995; Lamont *et al.*, 1995). There is no evidence for a seasonal phytodetritus fall, although few bottom photographs are available for this site. 8 box core samples were studied at this site.

The most southerly site, on the edge of the Cape Verde Abyssal Plain, is the French EUMELI oligotrophic site (EOS), a rising plain of 4500 - 4600 m in depth, centred on 20°N 30°W (Sibuet *et al.*, 1993; Cosson-Sarradin *et al.*, 1998). This area is hydrodynamically quiescent and has been subject to steady state sedimentary processes for at least the last 10,000 years (Auffret *et al.*, 1992). 6 box cores were studied from this site.

The final site, MAP, was originally intended as a control site for the DEEPSEAS programme in order to investigate the effects of seasonal phytodetritus at PAP. Prior to this programme being carried out, a considerable wealth of geological, chemical and biological data were obtained during a survey examining the feasibility of dumping nuclear waste at the Great Meteor East (GME) site at 31°N 25°W (Roe *et al.*, 1987). One of the conclusions of the survey was that the whole GME area had been subjected to considerable disturbance by recent turbidite events, hence the MAST investigators moved the study site east by 4° of longitude on to the Madeira rise. Unfortunately, as Rice *et al.* (1994) writes:

> *"Despite our efforts to avoid areas subjected to significant physical disturbance, subsequent data indicate that this site has also been affected by a recent turbidite originating from the channel between Madeira and the Canaries. This turbidite was initially estimated to be 200-300 years old but is now believed to be nearer 1000 years old... the more recent estimate reduces significantly the likelihood that the present-day benthos shows any residual effects of the turbidite, though this remains a possibility."*

The Madeira Abyssal Plain is probably the most extensively surveyed region of abyssal plain in the world (Weaver *et al.*, 1987). The abyssal plain (the location of GME) lies at a depth of 5400 m; the MAP site actually lies on the lower rise on the path of turbidite flow at 4900 m (Figure 1.7). Sediments in this area fall into two types - turbidites and pelagic sediments. Weaver and Rothwell (1987) made extensive maps of all the turbidites and concluded that the majority of them were formed by sea-level changes during interglacial - glacial transitions. However, the most recent turbidite (their turbidite *a*) has been dated to just 930 years BP (Thomson and Weaver, 1994) and appears to cover most of the MAP area to a depth of at least 90 cm. The extremely low sedimentation rates of 1-10 mm ky^{-1} (Weaver and Rothwell, 1987) have resulted in only a thin veneer of pelagic sediments lying above turbidite *a*.

Huggett (1987) describes the turbidite and pelagic sediments at GME as varying in two important factors - shear strength and organic carbon content. Turbidite sediments are more cohesive with a shear strength of 2-3 kPa, while pelagic sediments have values of only 0.3-0.6

kPa. Organic carbon content in the surface layers of the pelagic sediments is 0.12-0.15% and twice this in the turbidite sediments. Colley and Thomson (1985) found up to 1.75% organic carbon at 50 cm depth in some of the turbidite cores. In a separate study of multi-cores from the MAP site (4°W of GME), Wolff *et al.* (1995) found that normally labile lipids are present in high concentrations throughout the turbidite and that this was closely correlated with nematode abundance. However, organic carbon content was not significantly higher than that in pelagic sediments (in contrast to Huggett's results from GME). Undisturbed multi-cores taken from the area showed little evidence for any pelagic sedimentation above the turbidite layer. They concluded "*...that the sedimentary geochemistry appears to have been strongly influenced by the recent... deposition of a turbidite*". Bottom photographs at MAP show no evidence of a seasonal phytodetritus fall (Rice *et al.*, 1994; Thurston *et al.*, 1998). 5 box cores were analysed from the MAP site.

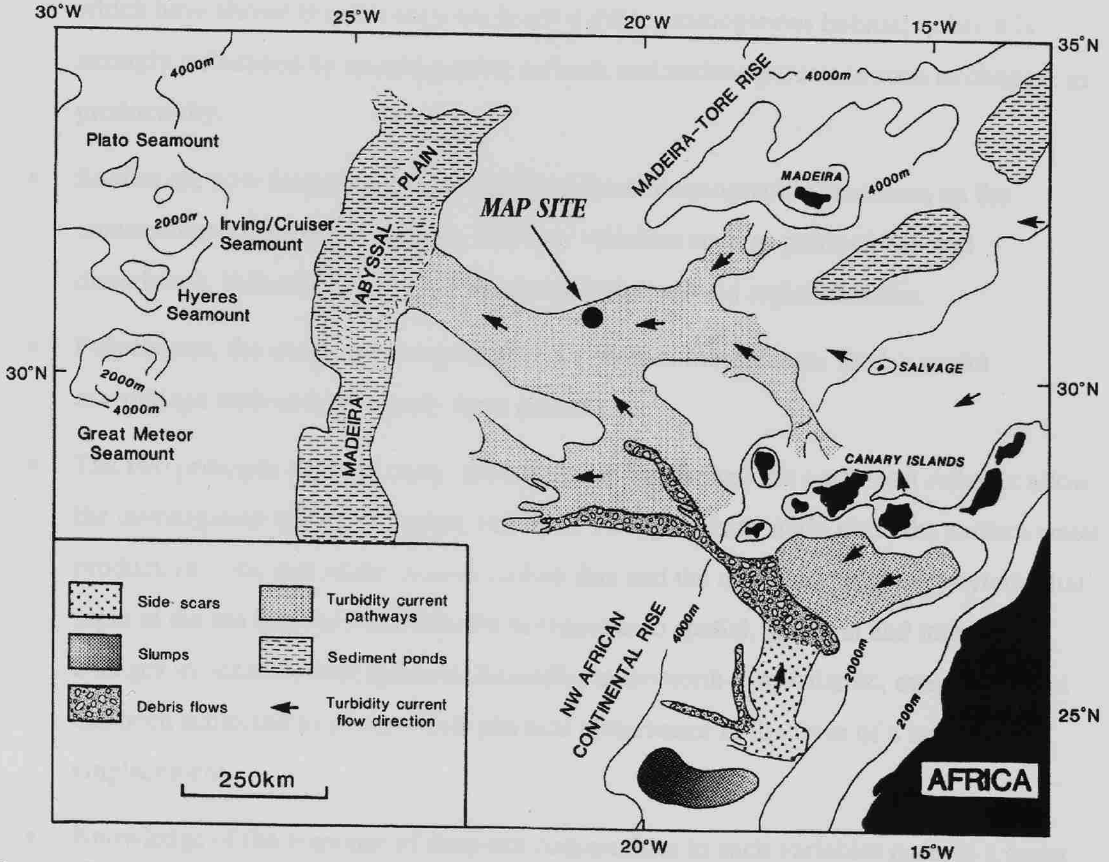

Figure 1.7 Map of the MAP region. Tracks of the various turbidite events are shown (after de Lange *et al.* (1987)).

Excluding the potential for turbidite impact at MAP for the moment, it can be seen that the most significant potential variable for these north Atlantic sites is the latitudinal gradient of productivity (Figure 1.5). Longhurst (1995) has categorised oceanic biogeochemical provinces based on CZCS satellite data summarised over a number of years. There is a general increase in productivity with increasing latitude. At PAP, productivity was 240 g C m^{-2} yr^{-1}, at TAP and MAP it was 122 g C m^{-2} yr^{-1}, at EOS, 106 g C m^{-2} yr^{-1} (Longhurst *et al.*, 1995). For the EqPac region, the yearly averaged Longhurst figures do not indicate such a dramatic trend – for the 0°N to 5°N sites lying under the equatorial divergence, productivity was measured at 113 g C m^{-2} yr^{-1}, for the 9°N / manganese nodule sites it was 107 g C m^{-2} yr^{-1} and at 23°N, 59 g C m^{-2} yr^{-1}. This overall productivity level is much lower than expected, given the similar nature of the benthic habitat at the equatorial phytodetrital sites with the north Atlantic PAP site. In Chapter 5, this apparent paradox is explored further in the light of the data available on POC flux and benthic macrofaunal abundance.

1.5 Summary

- The initial discovery of life in the deep sea was followed by the realisation that diversity at very small scales may be as high as it is in shallow-water habitats.
- These zoological studies of diversity have been complemented by oceanographic studies which have shown that the deep sea is not a stable, homogenous habitat; rather it is strongly influenced by oceanographic currents and surface processes such as changes in productivity.
- Studies are now focussing on the impact of these oceanographic processes on the communities of deep-sea animals, and how variables such as productivity and disturbance, influence diversity patterns on both local and regional scales.
- Polychaetes, the dominant component of the abyssal macrofauna, form a useful assemblage with which to study these patterns.
- The two principle areas of study, the equatorial Pacific and the north-east Atlantic allow the investigation of two important variables. Firstly, at both study sites, the surface water productivity, the mid water organic carbon flux and the nature and rate of 'phytodetrital' input at the sea bed vary latitudinally in response to spatial, seasonal and interannual changes in ocean current systems. Secondly, in the north-east Atlantic, one of the sites has been subjected to a large-scale physical disturbance in the form of a turbidite emplacement.
- Knowledge of the response of deep-sea communities to such variables permits a better understanding of local, regional and global biodiversity patterns.

2 THEORETICAL FRAMEWORK

This chapter has two purposes. Firstly, to review two important concepts relevant to this study, benthic-pelagic coupling and species diversity. Secondly, to outline a personal view of the philosophical framework appropriate to pattern-based deep-sea ecological studies.

2.1 Benthic – Pelagic Coupling in the Deep Sea

The concept of benthic-pelagic coupling is central to this thesis.

> *"The presence and persistence of life itself on the ocean-floor can be viewed as a response to organic inputs."*
>
> *- Gooday and Turley (1990)*

The deep sea is a food-limited environment (Dayton and Hessler, 1972; Hessler, 1974). With this in mind, it is a central premise that benthic abundance and biomass will be directly related to the amount of organic material reaching the sediment surface, whether originating from the pelagic layer or horizontal transport. A number of workers have shown this to be the case (Thiel, 1979; Carey, 1981; Rowe, 1983; Sibuet *et al.*, 1984; Sibuet *et al.*, 1989; Paterson *et al.*, 1994; Thurston *et al.*, 1994; Smith *et al.*, 1997; Paterson *et al.*, 1998; Thurston *et al.*, 1998; Glover *et al.*, 2001). In general terms, benthic biomass will be greater where surface productivity is highest (Gooday and Turley, 1990), although Paterson *et al.* (1998) showed how this relationship is not always clear, caused by variability in organic carbon export to the deep-sea floor. Quantifying this export production using sediment traps provides the 'missing link' to an understanding of deep-sea benthic dynamics.

In a wide-ranging review of POC flux data, Lampitt and Antia (1997) have shown that increasing productivity from 100 to 200 g C m^{-2} yr^{-1} leads to a corresponding increase in POC flux, but when surface productivity rises above 200 g C m^{-2} yr^{-1}, flux does not increase beyond 3.5 g C m^{-2} yr^{-1} (normalised to 2000m). So an increase in primary productivity may not always be reflected in an increase in POC flux to the seabed. This is because of the great distance the organic material has to fall (in the abyss, over 4 km) and the resulting action of mid-water variables such as horizontal movement caused by currents and consumption by pelagic animals.

The settling particles are of several main types: (1) large animal remains such as vertebrate carcasses; (2) large plant remains such as macroalgae, seagrasses and woody terrestrial material and (3) macroaggregates of microscopic plant and animal remains known as phytodetritus (Gooday and Turley, 1990). Submarine slides and turbidity currents may also inject organic materials into the deep sea (Huggett, 1987). At the EqPac sites 0°N to 5°N (hereafter termed the 'phytodetrital sites') and at PAP in the north Atlantic, there is evidence for a seasonal input of phytodetritus to the sea (Billett *et al.*, 1983; Smith *et al.*, 1996). Understanding the response of the benthic fauna to this phytodetrital input was a major goal of this study.

2.1.1 The response of benthic fauna to phytodetrital input

Phytodetrital material may be composed of a wide variety of planktonic remains, including diatoms, coccolithophorids, dinoflagellates, silicoflagellates, phaeodarians, tintinnids, foraminiferas, crustacean eggs and faecal pellets all embedded in a gelatinous matrix (Billett *et al.*, 1983; Lochte and Turley, 1988). Smith *et al.* (1996) reported intact diatoms of the species *Rhizosolenia* sp. in box cores from the EqPac sites that could be directly correlated with an observed bloom of this species in the surface waters (Barber *et al.*, 1994). They also reported that the material was 1-12.5% organic carbon by weight, which was 5-39 times greater than the organic carbon content in the associated seafloor sediments. For the north-east Atlantic BIOTRANS site (close to PAP), Lochte and Turley (1988) reported similar organic carbon contents of 0.56-7.8%. On the seafloor, phytodetrital remains at both Atlantic and Pacific sites were observed to accumulate in biogenic depressions, tracks and holes leading to a patchy distribution of the material. Phytodetritus is eventually consumed by motile surface deposit feeders, incorporated into the sediment through the action of bioturbators or washed away by deep-sea currents. The time-lapse photographs of the PAP site (Figure 1.6) indicate that the residence time of the material is on a time-scale of days to months.

The response of benthic megafauna to this patchy organic input has been well documented in the north-east Atlantic (Gooday and Turley, 1990). Billett *et al.* (1998) have shown how the holothurian *Benthogone rosea* may actively select and consume phytodetritus; the ophiuroid *Ophiomusium lymani* and echinoid *Echinus affinis* are also attracted to patches of phytodetritus.

Tyler *et al.* (1982) and Tyler (1988) have developed the hypothesis that a link exists between seasonal reproduction and the deposition of phytodetritus. This has been best documented for echinoderms, but the link has also been shown for isopods, bivalves, brachiopods, scaphopods, actinians and decapods (Gage and Tyler, 1991).

There have been few studies of the impact of phytodetritus *per se* on polychaetes, although there have been a number of studies of the general effects of enhanced food input associated with phytodetritus. Sibuet *et al.* (1989) and Paterson *et al.* (1994;1998) have shown how polychaete abundance is enhanced in the phytodetrital north-east Atlantic sites compared to more oligotrophic tropical sites. Smith *et al.* (1996;1997) demonstrated that phytodetrital EqPac sites exhibit enhanced macrofaunal abundance compared to non-phytodetrital ones. Some of these data are reanalysed in this study. The work of Grassle and Morse-Porteous (1987) on organically enriched settlement trays indicated the importance of opportunistic spionid and capitellid polychaetes in the deep sea. These species colonised the trays rapidly although they were not present in any abundance in the background community. Similarly, the dorvilleid polychaete *Ophryotrocha puerilis* is known to be opportunistic on a variety of organic remains, such as rotting wood and *Sargassum* weed.

It is possible that phytodetrital input may affect different polychaete taxa differently, and may influence the body size of those taxa. Levin *et al.* (1999) have examined macrofaunal processing of phytodetrital material from continental margin 850m sites. They observed the selective feeding of diatoms by polychaetes, especially paraonids of the genus *Aricidea,* maldanids and a nereid, *Ceratocephale.* Surprisingly, many of the small infaunal species in the deeper layers of the sediment were rapid consumers of the labile surface phytodetritus. Few studies have observed effects on body size of polychaetes as a whole, or of particular families. It is feasible that increased food input will enhance average body sizes as metazoans lay down storage compounds (for example, lipids); alternatively there may be a stronger selection pressure for a rapid reproductive pulse following phytodetrital input, and that body sizes in food poor environments will be larger owing to the scarcity of food and a greater requirement for food storage rather than reproduction. Examining such ecological trade-offs is problematic without time-series data; some inference can however be made from observations of spatial patterns.

The taxonomic difficulties of the small infaunal polychaetes has precluded many studies of the response in terms of diversity and reproduction. Only the larger motile scavenging deep-sea polychaetes have been described in detail; it remains to be seen whether these are a 'separate' fauna to the small infaunal species investigated in this study. The significance of the small infaunal species is that they contribute a large part of the biodiversity of the deep sea, hence an understanding of their spatio-temporal variability in abundance is essential.

2.2 Diversity

The purpose of this section is to introduce the current state of affairs regarding the patterns of species diversity and the processes that are thought to generate them. Firstly, a number of terms must be clarified. Biological diversity, or biodiversity, is a general term that is usually used to mean species diversity, although there is no reason why it should not also incorporate functional and genetic diversity (Figure 2.1). According to the United Nations Environmental Program, biodiversity incorporates elements of species diversity, genetic diversity and habitat diversity (UNEP, 1995). This study is concerned mainly with *species diversity*, although functional role has to some extent been investigated also. Species diversity can itself be subdivided into two important variables, that of the *number of species* in a sample (*species richness*) and the relative abundance of those species, or the degree of *equitability*. Changes in the degree of equitability can be caused by increases in *evenness* or *dominance*.

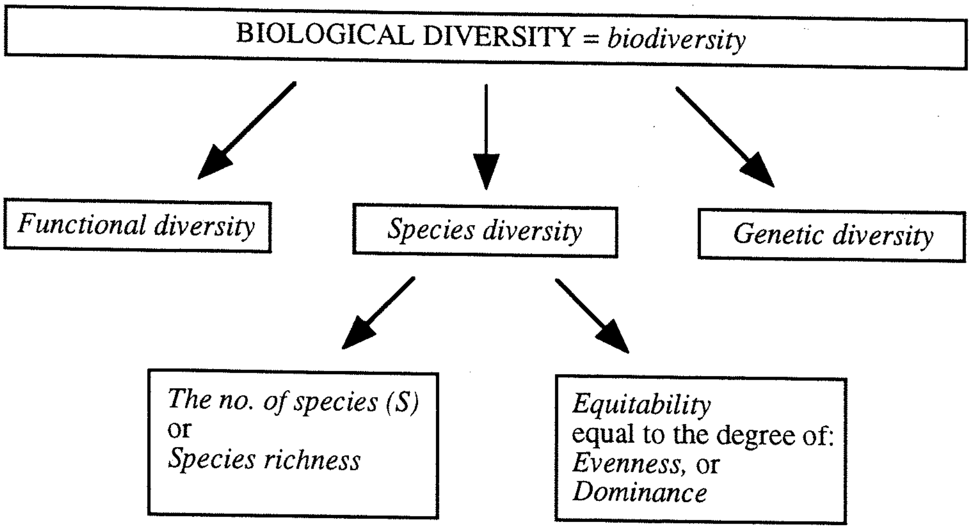

Figure 2.1 The taxonomy of diversity concepts used in this thesis.

Much of the last thirty years of research into species diversity has been about recognising certain characteristic patterns and using abductive inference to generate explanatory hypotheses for them.

These patterns of species diversity are remarkably consistent: Preston's (1962) log-normal distribution of species abundance's, the species-area curve, the latitudinal diversity gradient; the body size diversity pattern and the unimodal relationship between species diversity and productivity or disturbance. The discovery in the 1960's and 70's of these underlying numerical patterns of species diversity led many ecologists to think that there must be some unifying theory to explain them (Rosenzweig, 1995). But such a theory has eluded them. Each pattern has instead generated its own list of explanatory hypotheses; each hypothesis has its supporters and detractors. Recently, Rosenzweig (1995) has suggested that *area* is able to explain a great deal of these patterns, in that they are all to some extent based ultimately on species-area curves. But this view is not universally supported (Rohde, 1997).

2.2.1 Scales of diversity

The species-area curve is a very consistent diversity pattern, with the longest history and the most evidence to support it (Rosenzweig, 1995). Williams (1943) was the first to demonstrate it on a variety of scales, from tiny sub-hectare plots to entire biotas. The species-area curve is normally graphed in log-log space, so that a straight line is produced. The straight line has equation of form

$$\log S = z \log A + \log c$$

Where z is the slope, and c the intercept of the line. As this straight line is actually a curve in arithmetic space, both z and c are needed to describe the rate of increase in the number of species (S) with area (A). What should be noted is that if the sub-plots of the analysis are not contiguous (i.e. each plot is nested within each larger plot) the points do not follow this straight line equation, and it is not possible to determine z and c for the particular region being investigated. For this reason, evaluating species-area parameters in the deep sea is going to be very difficult, as the samples are not nested.

The two major problems of deep-sea diversity research are sampling artifacts and sampling design. The first are caused by undersampling and a failure to find enough individuals to find all the species in a particular area. The second is caused by pseudoreplication of samples and an unnested sampling pattern.

The first problem can be solved by using density-independent measures of species diversity, such as rarefaction, a randomised cumulative plot of species with individuals, or the sample-size independent version of Simpson's index, SI. These methods are described in Chapter 3. The second problem cannot be easily solved. Simply put, it is not yet possible to compare species-area curves between different areas of the deep sea or between the deep sea and shallow water. However, it is possible to be aware of the scale of diversity being compared, so long as the investigator remains aware that a species-area curve does exist (even if it cannot properly be measured).

Whittaker (1972) invented some terminology to describe scales of diversity, which have been reviewed by Gray (2000). Diversity for a single sample was termed 'point diversity'. Diversity for a series of samples within a habitat was termed 'alpha diversity'. The rate of species accumulation away from a point was termed 'beta diversity'. The diversity of a landscape or island was termed 'gamma diversity'. Finally, 'epsilon diversity' was the diversity of an entire region. It is clear that precise definitions of these parameters is very difficult, although Gray (2000) has attempted this:

Scales of species richness	**Definition**
Point species richness: SR_P	The species richness of a single sample unit
Sample species richness: SR_S	The species richness of a number of sampling units from a site of defined area (alpha diversity of Whittaker (1972))
Large area species richness: SR_L	The species richness of a large area including a variety of habitats and assemblages
Biogeographical province species richness SR_B	The species richness of a biogeographical province (gamma diversity of Whittaker (1972) and Rosenzweig (1995))
Other types of species richness	
Habitat species richness: SR_H	The species richness of a defined habitat
Assemblage species richness: SR_A	The species richness of a defined assemblage
Turnover diversity	Beta diversity of Whittaker (1972)

Table 2.1 Gray's (2000) taxonomy of species diversity concepts (adapted).

The most important distinction is that between Gray's 'scales of species richness' and 'types of species richness'. The former are artificial: a single sample, a summation of samples; the latter are real: the diversity of a rocky shore, the diversity of a muddy bottom. The scales of species richness measures are especially applicable to deep-sea situations, where habitat boundaries are unknown. In terrestrial systems, or in shallow-water situations, habitats can be much more easily observed and measures of habitat or assemblage species richness used. As Gray (2000) points out: "*Too often only point species richness, .. or sample species richness.. are calculated, whereas the study was of an assemblage or habitat...*". In other words, where habitats can actually be identified, research should focus on them.

This is not to say that measuring scales of diversity is not interesting. Gray actually advocates using alpha diversity to mean *only* the diversity of samples, and not to reflect an actual community. This is to attempt some objectivity, and is certainly relevant to the ongoing discussion of the comparative richness of the deep sea with shallow water. In addition, Gray suggests that most of the major gaps in our knowledge are associated with beta diversity. Getting proper measures of beta diversity for the deep sea and shallow water is the key to understanding their total species richness.

Rosenzweig (1995) dismissed most of these concepts of scales of diversity, focussing instead on the species-area curve. Marine biologists, on the other hand, need to worry much more about scales of diversity. This is because measuring habitat or assemblage diversity is so much more difficult. It is also because the species-area curve is such a universal phenomenon, so they know it will exist in the deep sea, even if they cannot measure it. The deep sea is not a series of box-cores. But a series of box-cores is all the information that is available. That information is useful, and can be compared with similar information from other areas of the deep sea, or with equivalent sampling methods in shallow water. So applying rigorous scales to diversity comparisons is not only useful, but allows much more objective comparisons to be made. Scales of diversity may appear artificial, but without defining them, the scientist is lost.

In the deep sea, it is possible to measure alpha diversity, estimate beta diversity, and guess at gamma diversity. All these measures of diversity are really just clues to what the species-area curve looks like.

2.2.2 Alpha diversity

Alpha diversity is usually measured in the deep sea as the diversity for a few square meters of sediment. Alpha diversity has sometimes been termed 'within-habitat' diversity for this reason. But there is no clear definition of what constitutes a habitat in the deep sea (Gray, 1997; Gray, 2000). The entire soft-sediment deep-sea benthos could be described as one habitat. For the purposes of this study, alpha diversity is diversity on the scale of a few box cores from a single location. The question we are asking of alpha diversity is – what variables are influencing the number of species found in a few square meters of sediment? In this thesis, I concentrate on the following two variables – *productivity-disturbance* and *regional enrichment.*

Productivity and disturbance are linked; not just in that both show the same unimodal pattern, but that both interact and affect each other. Huston (1979) realised this when he proposed the *dynamic equilibrium* model. But although the processes interact, they also have their own individual effects. Adding food may affect disturbance by increasing the number of bioturbators, but it also increases the size of the cake. Disturbance may be influenced by productivity, but it too has its own effects. The two variables must be treated together, but their influence teased apart.

Disturbance is perhaps the simplest ecological process to understand. The pattern is clear: diversity appears to peak at intermediate levels of disturbance. This is most noticeable on the rocky intertidal. Species living at the marine terrestrial interface take a pounding from the surf; some are protected by natural breakwaters, while some are exposed to the full force of the waves. At these two extremes, diversity is reduced. The sites exposed to intermediate levels of wave action have the highest number of species. This is the classic example of disturbance affecting alpha diversity. Connell (1978) spotted this disturbance pattern in rain forests and coral reefs. Sousa (1979) performed an early example of that rare thing in ecology, a hypothetico-deductive test on a rocky shore. Diversity was found to be highest on intermediate size boulders which were subjected to intermediate levels of disturbance. Intermediate disturbance levels in a patch-mosaic environment were proposed as the driving force for rocky intertidal species diversity (Paine and Levin, 1981).

The cause of the intermediary disturbance pattern is fairly well understood. It is the result of three processes – species disappearing in a patch as a result of competition; species disappearing in a patch as a result of disturbance, and species moving into these patches from well-stocked neighbouring patches (Paterson, 1993; Rosenzweig, 1995). These three dynamic processes operate on patches that never reach equilibrium state. Each patch shows either increasing diversity following a disturbance, or decreasing diversity caused by disturbance or competition. In high disturbance habitats, each patch is constantly held in check and no more than a few species can take hold. In intermediate disturbance habitats, species accumulate, but disturbance arises often enough to prevent competition from reducing diversity. In very low disturbance habitats, each patch accumulates species until competitive processes begin to reduce diversity.

Rosenzweig (1995) believes that disturbance theory is understood. This is probably true for the small temporal and spatial scales that rocky shore urchins and barnacles inhabit. On larger scales disturbance theory is less well understood, but it could be argued that this is because the word is used for too many different things. It is probably true that scientists should reserve the use of the word to small spatio-temporal scales.

Intermediate productivity patterns, according to Rosenzweig, are not really understood at all. Classic examples of unimodal productivity-diversity relationships come from mountain slopes where productivity is highest at intermediate elevations. Gradstein and Pocs (1989) data from the mountain slopes of Columbia forms a near-perfect hump, with peak diversities at 2000m. Other examples of productivity unimodal curves come from Tilman's (1982) work on plant nutrient enrichment – at very enriched sites, diversity was depressed. But Rosenzweig (1995) has cast doubt on these data. He suggests that the although diversity is depressed in small 0.1 ha plots, this is not really a pattern that can be applied to larger, real habitats.

Theories as to why productivity should increase diversity on the rising part of the unimodal curve are fairly simple. In contrast, a whole range of competing ideas exist for the explanation of why diversity should decrease with increasing productivity on the other side of the curve. Rosenzweig (1995) invokes Preston's (1962) observation of the log-normal distribution of species abundances as a theoretical underpinning for the increase phase of diversity. In this model, a theoretical 'veil line' exists below which species abundances are too low to cope with the pressure of accidental extinction. Assuming that the pressure of accidental extinction is highest on these rare species, increasing productivity reduces these chances of accidental extinction and increases the abundance of the rare species. If the log-normal distribution is to be maintained, then more rare species must arrive, hence increasing diversity. When populations are larger, more rare species can exist. The overall organic carbon cake is bigger. However, there is still considerable debate as to whether the log-normal is a real or an artifice of sampling (Lambshead *et al.*, 1983; Williamson, 1988; Rosenzweig, 1995).

There is convincing evidence that deep-sea sites lie on the rising phase of the unimodal productivity curve (Cosson-Sarradin *et al.*, 1998). Compared to shallow water areas, they are extremely food-impoverished hence it is unlikely that high productivity influences should affect diversity. What is interesting is that in the deep sea, diversity appears to peak at intermediate depths (Rex, 1981; Paterson, 1993). Some have proposed that this is caused by intermediate productivity levels, while others have proposed it is the result of intermediate disturbance levels (Dayton and Hessler, 1972). Huston (1979) combined the two in the dynamic equilibrium model, which suggests that the two unimodal curves can be combined to form a three dimensional 'hill'. An alternative explanation not related to productivity comes from the work of Etter and Grassle (1992) who suggested that habitat diversity (in this case sediment particle size variation) may be the best causal variable for the bathymetric gradient.

In this thesis, depth-related patterns are not investigated. Only abyssal sites greater than 3500m have been studied. Following from the study of productivity and diversity off the west African coast (Cosson-Sarradin *et al.*, 1998), the working hypothesis is that as abyssal sites must be food poor, any increases in productivity will cause increases in diversity, whether caused by productivity alone, or associated disturbance by bioturbators. The question of productivity and diversity on the decrease side of the hump is not addressed in this study.

Whatever the total organic carbon input, there must be species to subdivide it. Alpha diversity must be influenced not only by what processes impact it on the scales of centimetres and days, but on what species are available to colonise and contribute to diversity. *Regional enrichment* is the simple theory that suggests that local alpha diversity can be influenced by the total regional pool of species (Ricklefs, 1987; Cornell, 1993). Increase the number of potential colonisers, and diversity increases, so long as local ecological processes such as productivity and disturbance allow it. By analogy with a balls in the box scenario, the box, however big, contains only those balls that have been placed there. Assemblages that can accept more species are termed unsaturated assemblages, and their alpha diversity will be influenced by the total regional pool of species. Assemblages that cannot accept more species are termed saturated assemblages, and their local diversity is independent of regional diversity.

Unfortunately, demonstrating this simple concept is difficult. In the deep sea, all estimates of regional diversity (or gamma diversity) are usually based on measurements of alpha diversity, so a simple correlation is statistically problematic. It may not be appropriate to view the problem from a regional-centric standpoint if it is in fact the local diversity that is responsible for regional diversity. But Stuart and Rex (1994) have suggested that regional diversity is related to local diversity of prosobranch gastropods and that this relationship is mediated by the degree of planktotrophy. But it is not clear whether it is local diversity that is propping up regional diversity or the opposite.

Two prevalent spatial patterns of diversity can help this argument. Firstly, as described in the previous section, the species-area curve shows us how larger areas will be more diverse. Secondly, diversity increases over time.

Both these patterns are well established for terrestrial environments, but less so in marine ones. It may in fact be more of an assumption in the marine realm than an established fact. Diversity does show a trend to increase over time, but the reason it often does not do this is caused by other variables that are associated with increases in time, such as mass extinctions (Raup, 1992; Rosenzweig, 1995). But, all other variables aside, diversity has shown a general increase over geological time. With these two patterns in mind, it can be seen that one may expect much higher levels of regional diversity in the Pacific ocean than in the Atlantic ocean. The Pacific has an area of 166 million km^2 as opposed to the Atlantic's 82 million km^2. Additionally, the Pacific ocean dates back to Pre-Cambrian times, while the Atlantic has only been formed relatively recently following the break up of Pangaea in the Permian. It is a not unreasonable hypothesis that abyssal regional diversity will be higher in the Pacific than in the Atlantic.

Productivity, disturbance and regional enrichment come together with the theory of patch dynamics. Grassle and Morse-Porteous (1987) hypothesised that (1) spatio-temporal patchiness of food input against a low background level of productivity, coupled with (2) sporadic, small-scale disturbance events and (3) the lack of barriers to dispersal in the 'open' marine system would act to maintain species coexistence in a spatio-temporal mosaic of patches. In other words, patchy food input and disturbance are the factors that permit the coexistence of species; those species themselves stem from the total regional species pool.

This theory suggests the hypotheses that (1) species will be patchily distributed over the sea-bed, (2) areas receiving patchy inputs of food will show higher diversity than those that do not and (3) areas with higher regional diversity will show higher local alpha diversity. All these hypotheses are evaluated in this study.

2.2.3 Beta diversity, and total species richness

Beta diversity was a term invented by Whittaker (1960; 1975) in his study of the species richness of terrestrial north American forests along a latitudinal gradient. He defined it as *'the degree of change in species composition of communities along a gradient'*. Rosenzweig (1995) pointed out that beta diversity is equivalent to the slope of the species-area curve, although Gray (2000) counters this by saying that what Whittaker had in mind was the change in species identities along a gradient, not with species accumulations with area. Rosenzweig (1995) is correct that the slope of the curve is effectively a measure of beta diversity. But this is because it is the change in species identities along gradients that is a major cause of the species-area curve. Gray (2000) is correct that what Whittaker had in mind was not the species-area curve, but one of its underlying causes, that of the change in species composition with distance. Gray (2000) writes:

> *'... it is clear that beta diversity relates to the types of species contained and not to the numbers of species within two or more habitats.'*

In other words, beta diversity is not simply the slope of the species-area curve, but is a measure of the change in species composition with distance. But as the change in species composition (as a result of habitat heterogeneity) is a principal driving force of species-area curves then it is reasonable to suggest that the slope of the curve is a reasonable proxy for Whittaker's beta diversity. Alternatively, beta diversity could be redefined (Rosenzweig, 1995). For the moment, Whittaker's original definition is followed.

Understanding beta diversity in the deep sea is a crucial step. Currently, much of the discussions regarding deep-sea diversity rest on alpha diversity, and explanations for the bathymetric diversity gradient. No one doubts that at the level of a few square meters, there is a remarkably high number of coexisting, interacting species. But the real question is determining to what extent species composition changes across ocean basins. This is the clue to understanding regional diversity, and hence latitudinal gradients and ultimately evolutionary / speciation issues. Understanding these regional patterns is also important in that they themselves influence alpha diversity (see previous section).

Gray (2000) has called for research into the diversity of large areas of the marine system, and in particular a better understanding of beta diversity. In this study, estimates of beta diversity are to some extent limited by the fact that some of the samples have been studied by different taxonomists, although on the scale of 1000's of km beta diversity can at least be estimated.

The patterns of beta diversity in the deep sea are not well known, and the processes that generate them even less so. Polychaete reproductive biology in the abyss is virtually unknown, but it is likely that they are year-round non-seasonal breeders with both planktotrophic, lecithotrophic and direct development modes. Dispersal ability may be the key to understanding the pattern of beta diversity. Brown (1998), in a study of nematode alpha and beta diversity at the EqPac sites, indicated that there was a high degree of faunal turnover (beta diversity) between sites. Nematodes are thought not to have a planktotrophic dispersal phase (Lambshead, pers. comm.). If this were the case, it might be expected that they will show a higher level of beta diversity than polychaetes. It is also possible that different polychaete families will show differing levels of beta diversity if they exhibit different reproductive modes. In this study, the usefulness of drawing analogies of shallow water reproductive studies to the deep sea is assessed.

Understanding beta diversity is relevant to studies of the total species richness of biomes such as the deep sea. Grassle and Maciolek's (1992) observations of rates of faunal turnover along a transect at bathyal depths prompted them to propose the staggering figure of a potential ten million deep-sea macrofaunal species. The degree of endemicity is the important variable. For the north Atlantic sites, a compatible taxonomic dataset allows endemicity over a 2000 km scale to be investigated; in the equatorial Pacific a distance of 1000 km is possible. Differences in the degrees of beta diversity between the oceans have great implications for total (gamma) biodiversity issues.

2.3 The Role of Abductive Inference in The Scientific Method

The purpose of this section is to review the importance of hypothesis testing in science, and to indicate how a different philosophical approach can be of use in pattern-based studies such as this one. Though the achievements of science are undisputed, the methods by which science has achieved them leave many confused. The have been few attempts at a 'scientific' study of science, although David Hull's evolutionary approach to the study of evolution is a notable exception (Hull, 1990). Most studies of how science works have been left to the philosophers. Some philosophers may be scientists, but few scientists are philosophers.

Today, science does not require philosophy, its results surround us in their tangible form; abstract concepts of reasoning are left to a select few, who are mainly ignored. But in the late twentieth century, one philosophical idea was taken up to such an extent that it is now taught in schools as something called 'The Scientific Method'. This is the logical reasoning of Karl Popper known as hypothetico – deductivism (Popper, 1959). Popper's significant contribution to philosophy was to observe that theories cannot be proved true, only falsified or corroborated. In syllogistic logic:

*Start with hypothesis, **H***

*Deduce the predicted consequences, **O***

*If **O** is observed, then **H** is corroborated, but if not-**O** is observed, **H** is falsified.*

Hypothetico - deductivism is closely related to Aristotle's deductive logic: *all ravens are black, this bird is a raven, hence this bird is black.* Deduction is a form of reasoning that draws inferences from the general (the blackness of ravens) to the specific (a particular bird).

The hypothetico-deductive process is a necessary part of the journey from raw observation to useful conclusion but (in the author's view) it is often not the most important or difficult part, and may be subsequent to the critical discovery.

Before illustrating this point, and offering an alternative approach, it is of use to emphasise the importance of hypothesis and the many discoveries a hypothetico – deductive approach has provided. One of the most famous discoveries of all time was that of Christopher Columbus on his voyage across the Atlantic. It may not be a scientific story in the true sense of the word, but it has many of the features of a classic discovery in science. Columbus was completely obsessed with the idea that since the world was round, he could reach the Orient by sailing west. This, his hypothesis, was not completely original (as in many scientific stories) and he was certainly influenced by the stories of sailors who had been blown off course on past adventures. He met considerable difficulties in securing the financial support for his project, and when he finally set off he did not find the expected new route, but instead, a whole new world. Ultimately, he got little credit during his lifetime for his achievement, and he never realised the true significance of his finding. Despite all the evidence, he remained convinced to his death that he had actually proved his original hypothesis correct, and that the land he found was indeed the Orient.

The significance of hypothesis is its value in suggesting new avenues of research. The example quoted in the opening chapter was that of Edward Forbes' azoic theory. Forbes initiated deep-sea studies despite never taking any deep-sea samples below 230 fathoms (Menzies *et al.*, 1973). His hypothesis was instrumental in sending out future expeditions that, ultimately, disproved it.

> *"Hypothesis is the most important mental technique of the investigator, and its main function is to suggest new experiments or new observations"*
>
> *- Beveridge (1961)*

The value of hypothesis is undisputed, yet what is not appreciated is that most scientific work, even if initiated by a previous hypothesis, is concerned with coming up with new hypotheses, not falsifying existing ones.

What is remarkable is how much science has been achieved outside the hypothetico-deductive process. The most famous examples are those where chance discovery played a part. The circumstances leading to the discovery of penicillin are often described. Sir Alexander Fleming, working with plate cultures of staphylococci, noticed that the bacteria had died in some contaminated plates. Realising the significance of this observation, and following it up, he went on to discover penicillin, although its later development as a therapeutic agent was down to the work of Sir Howard Florey. Fleming was not testing a hypothesis. What he did was come up with a hypothesis to support his observations, using his own intuition and background knowledge.

Antoni Leeuwenhoek, the seventeenth century Dutch inventor of the first powerful microscope, did not hypothesise the existence of 'animalcules' (Protozoa and bacteria) before looking into a dish of pond water. Sanders (1968) did not *test* the stability-time hypothesis of species diversity in the deep sea. He made observations on diversity, and *formulated* the hypothesis. Sanders may well have been influenced by his earlier observations, and the hypotheses of others, but the significant scientific finding arose through the development of hypothesis, not the falsification of it.

The most obvious failing of the hypothetico-deductive process is that it ignores or distorts the role of careful observation as a source of knowledge (Halwes, 2000). It might be said that in the examples cited above, most of the discoveries were new and unexpected, hence it is unlikely that any preconceived theories were there to be tested. Most scientific observations will be less 'out of the blue' than these, especially in areas where a considerable depth of knowledge already exists. But this does not mean that observation is not still the most important part of the scientific process.

The hypothetico – deductivist approach, the only generally taught scientific method, is commonly applied to all disciplines. This includes those immature disciplines where there is little or no established theory (e.g. life on mars), those disciplines where there are competing established theories (e.g. deep-sea ecology) and those disciplines where there are well established, uncontested theories (e.g. molecular genetics).

In the first case of the immature scientific discipline, the lack of previous work makes coming up with a theory and hypothesis to test very difficult (as with Fleming, Leeuwenhoek and Sanders). Scraping together a theory, or erecting a null hypothesis serves no purpose and may well stifle interesting results. Stating that the raven is black before looking at it makes no difference to the final outcome – either it is going to be black or not. When researchers attempt to use the 'scientific method' on a new discipline, they restrict themselves, or have to go back and alter their original hypotheses based on the new data – making a mockery of the hypothesis testing procedure. A hypothetical researcher of ravens, on testing the hypothesis that ravens are black, might in fact discover that they are all purple. The original hypothesis of raven blackness serves no purpose other than to push the researcher into making observations. Leeuwenhoek did not, one presumes, stare down his microscope and note in his lab-book '...there is no evidence to support the hypothesis that there is nothing in the pond water'. Nor does one suppose that he subsequently re-wrote his introduction to suggest the hypothesis that there may be small forms of life in the pond-water, hitherto unknown. It is much more likely that he made simple, questioning *observations* - which is what most scientific methods that are actually used revolve around. Science proceeds, not through the falsification of hypotheses, but through observation, ideas, questions, understanding and intelligence.

> *"The scientist has no other method than doing his damnedest"*
>
> *- P.W. Bridgman (1955)*

A second type of discipline is one where there are already established competing theories. Deep-sea ecology is an example. A hypothetico – deductive approach could be employed in this case, for example, to test the hypothesis erected by Sanders (1968) that the deep sea is as diverse as tropical shallow-water habitats. There is nothing logically wrong about applying the hypothetico – deductive method to this situation (in contrast with the previous example). But the method is a gross simplification of the actual process of scientific discovery. All of the possible relationships between theory and evidence may lead to greater scientific understanding. Much important science is about the elucidation of surprising facts, and the use of those facts to generate further hypotheses. Much important science has sprung from the observations of the unsuspected – yet hypothetico-deductivism appears to offer little role for the unsuspected.

Gray (1994), setting out to test the hypothesis of Sanders (1968), discovered the surprising fact that species diversity on the continental shelf appeared to be as high as that in the deep sea. To sum up the result as 'Gray (1994) found no evidence to support the hypothesis of Sanders (1968)' would be to ignore virtually all that is of scientific value in the paper. The interesting and useful parts of the work concerned the authors' interpretation of his observations; namely that it is the method of diversity measurement that is of importance, and that diversity may well be underestimated at shallow water sites for these reasons. In other words, the surprising fact has led to a series of observations and the erection of further explanatory hypotheses to account for them. A surprising fact may support a theory, be at odds with it or maybe there was no theory at all. Scientific understanding is amplified by all of these scenarios.

The third type of discipline is the one where there is already an established theory. For example, the theory of molecular genetics is well understood. The human genome is sequenced. Scientists working in this field are not testing the theory of genetics, they are simply doing Kuhnian 'normal science' in a post-paradigm shift world. Most of what they do will be exploratory - observations of new and surprising facts that do not currently fit with the whole theory. But the basic theory will not be questioned, the surprising facts are mysteries that will be ultimately elucidated through questioning, learning and the generation of further explanatory hypotheses on top of the established theory.

Theories *are* used to generate hypotheses. Hypotheses *are* tested. But Popperian hypothetico – deductivism is a simplification of how science proceeds. Science almost never proceeds through the falsification of theories. It proceeds through an increase in scientific understanding, an increase in the number of observations. Primarily, it proceeds through people thinking up new explanatory hypotheses (putative theories) to account for patterns and effects. They can do this through the power of learning, intelligence and above all, observation.

The question arises as to why hypothetico – deductivism is still so widely taught as *the* scientific method. That it was an important and influential development in the theory of logical analysis there is no doubt. But it was no more important than many of the other developments in the philosophy of logic that occurred in the 19th Century. It seems probable that the simplicity of the idea and the ability to sum it up in a sentence has contributed to its attraction. The real scientific method, if it exists, cannot be summed up in such a way. The danger of hypothetico – deductivism is that it ignores or belittles much that is important about scientific research. Scientists who blindly follow the hypothetico – deductive argument may be tempted to suppose that knowledge can be generated by rote: – 'create theory -> generate hypothesis -> test hypothesis -> answer true or false'. While that may be a correct, if partial, description of the scientific process, to place it centre-stage may ignore the possibility that the critical and interesting sequence in this set of operations was the creation (or selection) of the 'theory' upon which to operate. What matters most in scientific research is individual intelligence, observation and creativity. There may not be a scientific method, but there are scientific methods.

If there is one philosopher who has something useful to say on the logic of scientific discovery it is Charles Sanders Peirce (1839-1914) (Hanson, 1961). Peirce, a mathematician, distinguished between the ideas of abduction, deduction and induction. His definitions of deduction and induction where similar to those that had come previously. Abduction, however, was a new logical syllogism, and is most relevant to what is a commonly used scientific approach:

> *The surprising fact, C, is observed;*
>
> *But if A were true, C would be a matter of course.*
>
> *Hence, there is reason to suspect that A is true.*

Abduction, or abductive inference, is so called as the hypothesis with the most explanatory power is 'abducted' from the others. For example, a man walks into a room and discovers a smashed window with a stone lying on the floor. This is the surprising fact, C. He *conjects*, the hypothesis, A, that the stone has flown through the window and smashed it. If A were true, C would be a matter of course, hence there is reason to suspect that A is true. The Peircean notion of abductive inference is very close to the cognitive process most commonly used by scientists – observation, suspicion and discovery.

Peirce's taxonomy of inference proceeds as follows. Firstly, there is abduction, or hypothesis generation through conjecture. Surprising facts, quantitative or qualitative are observed and the observers own intelligence and learning resources used to *abduct* the hypothesis with the most explanatory power. The hypothesis with the most explanatory power is usually the most parsimonious explanation, according to the premise of William of Occam (1285-1349), or 'Occam's razor'. Secondly, deduction follows – this is the evaluation of hypothesis, or the hypothetico – deductive method. Using the same analogy, the observer may experiment by throwing the stone through another window to see if the same result is generated. Finally, induction is possible, or the extension of inference from the specific to the general - stones are heavy, hard and will when thrown at a particular velocity, smash windows.

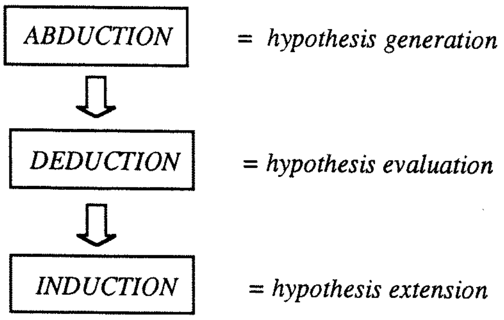

Figure 2.2 Peirce's taxonomy of inference

The hypothetico – deductive method ignores abduction, which is the most important part of the process. There is no doubt that scientists do frequently set out to test hypotheses; but that only signals the start of an investigation. Many of the discoveries and advances in science are created through hypothesis generation, or abduction. Hypothetico-deductivism may be a valid and logical basis for analysis, but it is not the only scientific method. In addition, there is little to be gained by structuring non-experimental, pattern based studies into pseudo-hypothetico-deductive ones, and there is probably much to be lost.

> *"To have one's ideas appear compelling to the psychological establishment in the late twentieth century it is necessary, because of the esteem in which hypothetico-deductivism is held, that the ideas be expressed as theory-generated hypotheses that have undergone the 'ordeal' of experiment."*
>
> *- Cheyne and Tarulli (1990)*

The inference of phylogeny through cladistics is a classic example of the use of abductive inference over other types of reasoning (K Fitzhugh, pers. comm.). The aim of cladistic analysis is to causally account for shared character states amongst taxa. It is a common misconception that a cladistic analysis of shared character states (putative homologies) using parsimony, maximum likelihood or other common similarity measures is somehow a hypothetico – deductive 'test' of these homology hypotheses. In fact, cladistics operates entirely within the abductive inference rule, and does not venture into deduction at any point. Cladistics is about selecting the hypothesis with the most explanatory power. Using the analogy of the stone and the window again, it can be seen that cladistic analysis is about generating all the possible reasons for the stone to be lying on the floor (it went through the window, it just happened to be there while the window broke for some other reason, somebody put it there after first smashing the window etc.) and selecting the one with the most explanatory power, which is generally, the most parsimonious one. Cladistics does not experiment by throwing the stone.

Abductive inference can actually be split into further categories of reasoning. Take the example of Grassle and Morse-Porteous' (1987) theory of patch-dynamics applied to the deep-sea benthos. In it they coupled their background knowledge of deep-sea biology (in particular the importance of spatio-temporal mosaics of species successions demonstrated in a previous paper) to their observations on the colonisation of azoic sediment trays to form a delimited set of explanatory hypotheses. These explanatory hypotheses were the importance of patchy organic input, the presence of small-scale disturbances and the openness of deep-sea populations. These explanatory hypotheses were composited to form a general hypothesis of patch-dynamics as an important community structuring force. Actually, in the paper, the authors did in fact follow the hypothetico – deductive reasoning, stating their hypotheses in the introduction – but the important parts of the paper were not the falsification or not of those hypotheses, but the generation of new hypotheses at the end of the paper based on abductive inference of their observations. This example has been cited as it is clearly an 'experimental' type of deep-sea study. But the important results to come out of it were based on abductive inference and not on hypothesis testing.

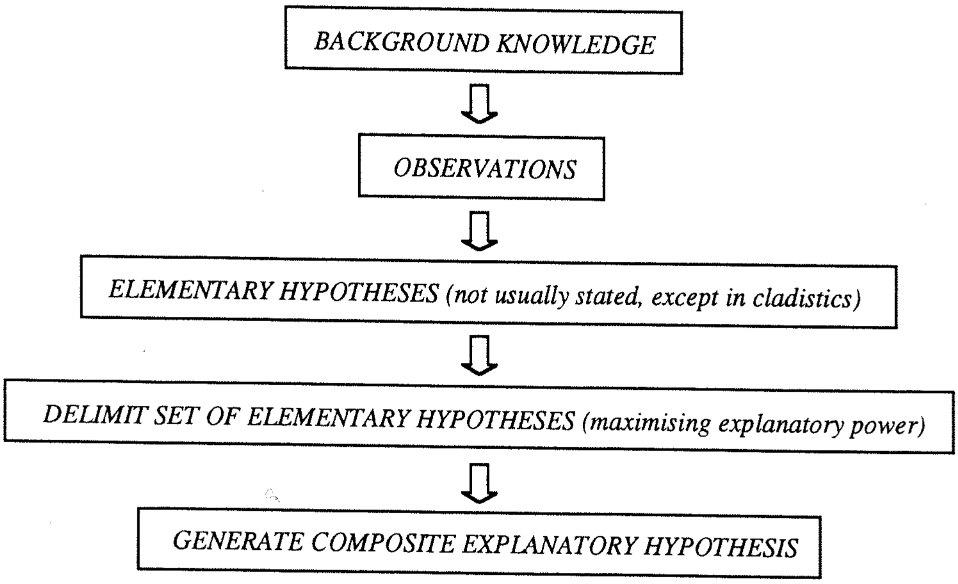

Figure 2.3 The method of abductive inference. Background knowledge is applied to observations to generate hypotheses with the most explanatory power. In cladistic theory, the 'elementary hypotheses' are formed (all possible phylogenetic reconstructions) and the most parsimonious selected.

The following sections of this thesis follow the philosophical approach highlighted in this section. Where background knowledge suggests testable hypotheses, they are indicated. Where knowledge is limited, no attempt is made to frame questions in a hypothetico-deductive way. In Chapters 4, 5 and 6 the observations are presented and discussed in the light of the background knowledge and explanatory hypotheses generated. In Chapter 7, a conclusion and composit explanatory hypotheses put forward.

2.4 Summary and Main Objectives

- Benthic-pelagic coupling is a central concept in this thesis, and the review of background knowledge suggests the following hypothesis:

  > *Benthic abundance is closely correlated with deep-water POC flux and surface productivity in both the Pacific and Atlantic Oceans.*

- Species-area curves for deep-sea sites are an elusive goal; understanding diversity on the artificial scales of alpha, beta and gamma is the only way for meaningful comparative studies to be made. Habitat and/or assemblage species richness cannot be estimated, unless these concepts can be defined for the deep-sea.

- Theoretical ecology suggests the following hypotheses regarding alpha diversity:

  > *Productivity and alpha diversity will show a positive linear relationship in food poor abyssal sites.*
  >
  > *Areas receiving patchy inputs of food will show higher alpha diversity.*

Alpha diversity and small-scale disturbance will show a unimodal relationship.

- The regional enrichment theory suggests the hypotheses:

  Alpha diversity is enhanced by regional enrichment

- There have been few studies of beta diversity for the abyssal ecosystem. The question arises:

  What is the scale of beta diversity (faunal turnover) and does it vary between ocean basins and between different taxa?

- Gamma diversity issues are problematic without an understanding of beta diversity, hence:

  Can an estimate of total species richness be made for the abyssal polychaete fauna in the Atlantic and Pacific oceans, based on an understanding of faunal turnover on the scales of 1000-2000 km?

3 METHODS

3.1 Sampling and Collection

3.1.1 Sampling design

In this study, data have been drawn together from eight different cruises using six different ships over a period of about 17 years. The sampling, sieving and sorting of material was carried out by several different labs and many people. The identifications have been performed by three different taxonomic specialists, including the author. Sampling design must, to some extent, be assessed after the event, and inferences made from statistical analysis treated as necessary. Nevertheless, in the last thirty years, standardisation of methods on ship and in laboratories has allowed much more freedom in the ability to draw data together from different cruises. Although the deep sea is often said to be 'difficult' to sample, the nature of the benthic habitat and the use of advanced coring devices allows very precise samples to be taken. This cannot always be said of the more complex three dimensional habitats that are found in shallow water and the terrestrial ecosystem. The large amount of money, precise planning and great effort that goes into a month's oceanographic cruise usually results in a set of very high quality samples. Unfortunately, time constraints and the difficulty of re-sampling an area once the cruise has finished mean that often the limiting factor is the number of samples, even if they are of high quality.

The nature of deep-sea sampling methods predisposes them to the problem of pseudoreplication. Hurlbert (1984) recognised this problem with what he termed 'mensurative' ecological experiments. These are experiments where the only treatment is a change in space or time and there is no manipulation by the experimenter. These are the most common deep-sea experiments, and this study is one of them. In this case, the degree of phytodetrital food input to the polychaete community has not been altered, rather, the community in areas that receive different amounts of phytodetritus has been measured. The pseudoreplication issue arises as deep-sea sampling sites are clustered, rather than randomly distributed across the gradient or boundary of interest. The *sites* may be distributed randomly, but the *samples* are not, their position is pre-determined by the choice of just a few sites, hence they are not true replicates. Pseudoreplication is widespread across the literature (Hurlbert, 1984). In this case, were pseudoreplicates to be removed from the analysis there would be insufficient data to examine. The caveat remains, but it would also be inappropriate to ignore significant differences for the reason of pseudoreplication alone. Pattern-based studies such as this are inevitably restricted by their design, but are not in themselves devoid of value for reasons of statistics alone.

In sections 1.3 and 1.4 the physical, chemical and biological regime of the sampling sites was introduced. The principal theoretical framework of this thesis is that latitudinal changes in productivity in the Pacific and Atlantic oceans have a profound impact on the abyssal benthos. Both the EqPac and north Atlantic sampling programs were designed from the outset to test this hypothesis, but the DOMES, PRA and ECHO sites were designed to investigate the effects of physical disturbance by deep-sea dredging for manganese nodules. Furthermore, it is now known that one of the north Atlantic sites, at MAP, has also been subject to physical disturbance (Glover *et al.*, 2001). At DOMES, PRA and ECHO, there is little evidence to suggest that physical disturbance is important (Wilson and Hessler, 1987). So these sites may also be used to test for the influence of productivity, as they lie further north than the more productive EqPac sites. In the north Atlantic, the sites also lie on a gradient of productivity, but the effect of physical disturbance at MAP must also be tested; this is discussed further in section 6.3.4.

3.1.2 Collection of material

Table 3.1 details the sampling locations, collection method, water depths and collection dates. The thirteen EqPac samples were collected in November 1992 aboard the R/V *Thomas Thompson* (TT013) by Dr Craig Smith of the University of Hawaii (Smith, 1992). The four HOT station samples were collected in July-August 1992 and February 1993 also by Dr Craig Smith. The forty-seven DOMES A samples were collected in 1977-78 aboard the O.S.S. *Oceanographer* (Piper and Blueford, 1982). The fifteen ECHO 1 samples were taken in April 1983 aboard the R/V *Melville* (Spiess *et al.*, 1987; Thistle and Wilson, 1996). The fifteen PRA samples were collected in October 1989 aboard the R/V *Moana Wave* (Thistle and Wilson, 1996).

In the north Atlantic, the five samples from PAP were collected in May 1991 aboard the RRS *Challenger* (Rice *et al.*, 1994). The eight box cores from TAP were collected in October 1989 aboard the RRS *Discovery* (Gage *et al.*, 1995; Lamont *et al.*, 1995). The five box cores from MAP were collected in August 1990 aboard the RRS *Discovery* (Rice *et al.*, 1994). The six box cores from EOS were collected in September-October 1993 aboard the RRS *Discovery* (Rice, 1993).

At all sites, a smallest sieve size of 300 μm was used; this has become the standard for deep-sea benthic research. At the north Atlantic sites, a 250 μm sieve was also used, but only those polychaetes retained on the 300 μm size examined.

It should be made clear that only the material from the EqPac, HOT and MAP sites (22 samples) was examined and identified by the author. Material from PAP, TAP and EOS (19 samples) was examined and identified by Gordon Paterson of The Natural History Museum, London. Material from DOMES A, ECHO 1 and PRA (77 samples) was examined and identified by Kirk Fitzhugh and Kristian Fauchald of the Smithsonian Institution, Washington DC. The difficulty of sampling the deep-sea bed makes re-analysis of existing data an essential part of any study; in this case the fortuitous fact that all 118 samples were collected by USNEL spade-box cores makes this the largest comparative analysis of abyssal polychaete assemblages to date.

Site	Position	Depth	No. of Cores	Date Collected
EqPac 0°N	0°N 140°W	4300m	3	Nov-92
EqPac 2°N	2°N 140°W	4400m	4	Nov-92
EqPac 5°N	5°N 140°W	4400m	3	Nov-92
EqPac 9°N	9°N 140°W	4900m	3	Nov-92
HOT 23°N	23°N 158°W	4800m	4	Aug-92 / Feb-93
DOMES A	8°27'N 150°47'W	~5000m	47	1977-1978
PRA	12°57'N 128°19'W	4800m	15	Oct-89
ECHO 1	14°40'N 126°25'W	4500m	15	Apr-83
PAP	48°N 16°W	4800m	5	May-91
TAP	38°N 11°W	5035m	8	Oct-89
MAP	31°N 21°W	4900m	5	Aug-90
EOS	20°N 30°W	4600m	6	Oct-93

Table 3.3.1 Position of sites, depth, number of samples (all are USNEL spade box cores) and date of collection.

3.1.3 The USNEL spade box corer

The United States Naval Electronics Laboratory (USNEL) spade box core has become a standard tool for deep-sea benthic research. The box core was originally developed by Reineck (1958). The USNEL box core version was modified and enlarged for marine biology by Hessler and Jumars (1974). The main advantage of this enlarged core was that it offered the precision of the original Reineck core but with the advantage of being large enough to sample impoverished deep-sea sites. This original version of the box core has been subsequently modified, principally by Robert Hessler and Sandia Laboratories; newer versions are sometimes referred to as Hessler-Sandia box cores. They are manufactured by Ocean Instruments Inc., San Diego, California.

The box core collects a 0.25 m^2 section of the sea-bed with a relatively undisturbed sediment-water interface. It is a simple device consisting of a detachable open ended steel box attached to a weighted column (Figure 3.1). On impacting the sea bed the box sinks into the sediment; how far it sinks is dependent on the compactness of the mud and the weight of the corer, which can be altered. The spade is released and swings down into the sediment and seals the bottom of the box against a rubber seal. Small doors at the top of the box also spring shut and the entire core is then lifted out of the sediment and brought to the surface. Once on deck, the box can be detached from the rest of the coring device and taken for processing while another core is dropped. A good core will have clear overlying water and an undisturbed sediment surface; the top water should be at the same ambient temperature as the bottom water indicating that there has been no mixing during the retrieval process. Most of the fauna is usually present in the top water and the first few cm of the sediment. The presence of motile megafauna (e.g. Holothurians) on the sediment surface would be a good indication of a successful core.[3]

At some of the sites (EqPac, HOT and TAP) the 'vegematic' modification of Jumars (1975) was used. Metal sub-dividers are inserted into the box so that the whole core is composed of 25 sub-cores. The potential advantage of this is that there is less mixing of the top water on retrieval; also some of the sub-cores can be used for meiofaunal or chemical analysis while leaving the rest for macrofauna. The potential disadvantage is that there is an enhanced bow-wave effect. At the EqPac sites 18 out of 25 sub-cores were used for macrofauna, at HOT 15 were used and at TAP only the 'inner' 9 were used. This change in sampling area is taken into account during analysis and interpretation of the results.

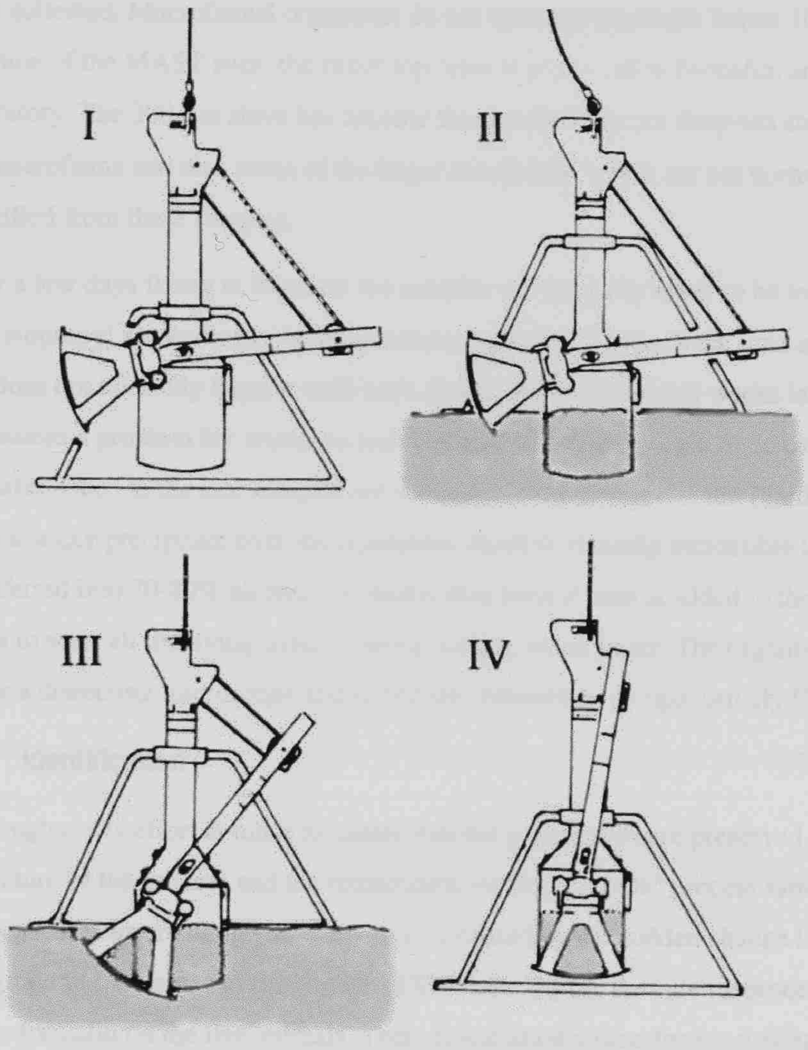

Figure 3.1 USNEL box core - schematic diagram showing retrieval of a 0.25m^2 section of the seabed (modified from Gage & Tyler (1991))

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[3] Although I did not take part in any of the cruises where material was collected for this study, I gained considerable experience in the use and processing of USNEL box cores on a benthic cruise off the west Antarctic peninsula continental shelf in March 2000, for which I am grateful to Dr Craig Smith of the University of Hawaii.

3.1.4 Laboratory processing

Processing of a box core for macrofauna proceeds as follows. The top water is drained off using a clear plastic hose onto a 300 μm sieve. The whole core is then moved over to the wash table, where a filtered sea water system has been set up. The first layer (0-1 cm) of sediment is then sliced using small trowels and placed into a large 'elutriating' bucket. Water is gently washed into the bucket and a small drain at the top of the bucket is directed over a 300 μm sieve where the elutriated material collects. Great care is taken not to lose any sediment or for the rate of flow to become too vigorous, potentially damaging the animals. The process is continued until all the fine sediment has passed through the sieve; the residue is then washed carefully into plastic jars and fixed in 4% buffered formalin. The same procedure is followed for the 1-5 cm and 5-10 cm layers. At the PAP, TAP, MAP and EOS sites, 0-1, 1-3, 3-5 and 5-10 cm layers were collected. Macrofaunal organisms do not normally penetrate below 10 cm in abyssal sites. At some of the MAST sites, the entire top layer is preserved in formalin, and sieved back in the laboratory. The 300 μm sieve has become the standard size for deep-sea studies as it collects all the macrofauna and also some of the larger meiofauna, which are not normally counted or identified from these samples.

After a few days fixing in formalin the samples are normally ready to be transferred to a 70-80% isopropyl alcohol solution for permanent storage. Owing to the time constraints on ship, this does not normally happen until back in the laboratory several weeks later. This is sometimes a problem for crustacea and molluscs which may begin to de-calcify in the acidic formalin. Once in the lab, samples are washed in fresh distilled water (hard water and formalin form a sticky precipitate over the organisms which is virtually impossible to remove) and then transferred into 70-80% alcohol. Normally rose bengal stain is added to the samples for 24 hours to stain all the living tissue, making sorting much easier. The organisms are then picked under a dissecting microscope and sorted into taxonomic groups, usually Class.

3.2 Identification

Although every effort is made to ensure that the polychaetes are preserved in good condition, the nature of the process and the requirement on ship to 'bulk' process samples, means that many specimens are damaged. This may be caused by the sudden change in temperature on bringing the specimens to the surface (1°C to over 20°C), the sieving process itself, or the effect of the formalin on the live animals. There is not usually time for specimens to be collected individually and 'relaxed' in $MgCl_2$ as suggested by Fauchald (1977). Also, the addition of a relaxant would require an extra sieving stage, which would cause more damage and possibly negate any advantages gained through relaxing. Polychaetes are especially fragile; deep-sea specimens often fragment, lose their palps and shed branchiae. This limits the number of characters available to the identifier.

There have been relatively few taxonomic studies of abyssal polychaetes. The first were from the material collected by HMS Challenger in 1873-1876 (McIntosh, 1885). Chamberlin (1919) worked on the central Pacific material collected by Alexander Aggasiz. Some polychaetes were described from the Swedish deep-sea expedition (Eliason, 1951). Jorgen Kirkegaard worked on the material collected by the Galathea Deep-sea trenches expedition (Kirkegaard, 1956). Olga Hartman and Kristian Fauchald did a considerable amount of work on deep-sea polychaetes in the 1960's and 70's using Sanders' material from the Gay Head-Bermuda transect (Hartman, 1965; Fauchald, 1970; Hartman and Fauchald, 1971). Jorgen Kirkegaard has also published several new species from the eastern Atlantic bathyal and abyssal depths (Kirkegaard, 1980; Kirkegaard, 1982; Kirkegaard, 1983; Kirkegaard, 1994). In the Pacific, K Fauchald has also worked on deep-water material off western Mexico (Fauchald, 1972). Levenstein (1971, 1972) has worked on several abyssal species collected by Russian sampling programmes in the central Pacific.

Most of these studies have been of the larger polychaete specimens collected by trawls and dredges. Many of the small infaunal species retained on a 300 μm sieve are likely to be undescribed. In this study efforts have concentrated on getting as much data on diversity as possible, rather than attempting a monographic-style work on the abyssal fauna. For this reason, species identified have been given a unique code number (*Aricidea* sp. 601, *Sigambra* sp. 008 etc.) and no attempt has been made to find a name for them. In cases where the genus was also unclear, just the family and the species number are given.

Only providing a number for a new species rather than a name has some disadvantages. Datasets generated this way are unique, and cannot be compared for faunal similarity with datasets generated by different taxonomists using different species lists. However, publishing detailed species descriptions for 170 species from 30 different families is beyond the scope of this PhD. K Fauchald (pers. comm.) has pointed out that it is simply not possible for a polychaete taxonomist to specialise on more than one or two families. Assigning names to species without enough specimens or with inadequate descriptions would add further confusion to the taxonomic literature. Nevertheless, to fully understand the ecology of the deep sea, the biology of the animals that live there must be investigated, and this can only be achieved by first doing the necessary taxonomic work (see Chapter 4).

3.2.1 Laboratory procedure[4]

The small size of deep-sea polychaetes requires certain 'adaptation' of traditional shallow-water taxonomic techniques. The specimens were initially sorted to family under a dissecting microscope. Standard keys were used (Day, 1967; Fauchald, 1977). Whole worms and

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[4] This is the procedure for the identifications carried out by the author for the EqPac and MAP material, identifications for the other sites were carried out by different taxonomists.

fragments with heads only were picked out. For some very small specimens, a high-power microscope was needed to confirm the family through examination of the chaetae. Indeterminants were also picked out for later examination, and they were also counted for the abundance values. The specimens were placed in glass "Durham tubes" which were then placed inside a larger vial filled with 80% isopropyl alcohol. Movement and manipulation of the specimens is done using softly-sprung forceps, which do not damage the specimens.

Families were then taken in turn and identified to 'species' level. Essentially, this is the point at which no further morphological differences can be ascertained. For most specimens, the whole worm was temporarily mounted on a cavity slide in a mixture of alcohol and glycerol and examined under a high-power interference contrast Olympus BH-2 microscope. Only for some of the larger specimens was a traditional parapodial preparation possible. In many cases, the oil immersion objective was used; this required the dissection of a small transverse-section of the worm and mounting on a flat slide.

For each specimen, drawings, measurements and notes were taken and the specimen was given a unique species number. In most cases it was also possible to identify the genus to which the specimen belonged. A unique specimen code number was assigned; this proved extremely useful for quickly locating previously examined material for comparison. For the more 'difficult' families, such as the cirratulids and paraonids, specimens were re-examined several times with potential conspecifics before species assignments could be made. For two of the families, the Pilargidae and Cirratulidae, a more detailed taxonomic assessment using scanning electron microscopy was carried out; this is described in chapter 4.

3.2.2 Body Size

Body size was measured in a number of ways. The main problem was that many of the worms were fragmented. Measurements were made with the aid of a 'camera lucida' type drawing tube attached to an Olympus BH-2 or ZEISS dissecting microscope. For each specimen, the maximal prostomial width, the first chaetiger width, the tenth chaetiger width, the length of the first ten chaetigers, the total number of chaetigers and the total length were measured. For many of the specimens not all of these measurements were possible. The philosophy was to measure as many things as possible and to evaluate them as predictors of total worm volume. Volume may be a more useful measure of how much the animal has grown compared to chaetiger number; polychaetes do not add segments in a linear fashion. Volume was calculated on the assumption that the worms are cylindrical.

3.3 Analysis

3.3.1 Productivity, abundance and size

A consistently applicable method of measuring surface productivity was sought. Although a huge number of oceanographic studies have measured production directly using the ^{14}C tracer technique, its use for comparative studies is problematical (Longhurst *et al.*, 1995). Satellite derived measurements of ocean chlorophyll pigment have become more widely used for regional studies of production.

The SeaWIFS and CZCS satellites operated by NASA offer data on the surface productivity of the oceans on the internet[5]. These data were used extensively for EqPac planning (Feldman *et al.*, 1992). At Rutgers University Institute of Marine and Coastal Sciences, the chlorophyll data from the SeaWIFS satellites has been converted to measurements of oceanic primary productivity using the method of Behrenfeld and Falkowski (1997). These primary production maps have been re-analysed for this study using the computer program *Adobe Photoshop 5.5* for Apple Macintosh. In *Photoshop*, provinces of ocean colour are obtained using the *select color range* command that highlights a specified range of colours in the RGB spectrum. Clicking the mouse on the position of the sample site immediately selects all areas of similar levels of productivity on the world map and on the productivity scale bar, allowing the user to read the level of productivity for a particular site. Furthermore, by using the sub-command *fuzziness* the user can increase or decrease the width of the colour range, allowing one to select broader or narrower ranges of productivity. When a range of productivities was observed, the median value was used for the subsequent analyses. *Fuzziness* was left at a level of 90.

The data on abundances were manipulated in *Microsoft Excel 98* and exported to *Statview 5.1* for analyses. The samples from TAP and EqPac (slightly smaller than 0.25 m^2) were corrected for sampling area. Simple linear regressions were used where appropriate, in addition, a LOWESS (locally weighted scatterplot smoother) smoother was used. This method is a simple way of illustrating the shape of a non-linear plot where linear regression is inappropriate; it is not a statistical 'test' of the data.

Abundance data were tested using the non-parametric Mann-Whitney test. The body size data were log transformed for analysis of variance (ANOVA) and t-test. Fisher PLSD post-hoc tests were used to evaluate the relationship between treatments.

3.3.2 Alpha diversity

The computer program *BiodiversityPro* (McAleece *et al.*, 1996) was used to analyse diversity data. Alpha diversity was estimated using diversity indices, rarefaction and the cumulative

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[5] http://seawifs.gsfc.nasa.gov/seawifs.html

number of species with individuals (randomised). Any method of measuring alpha diversity in the deep sea must be sample-size independent.

Diversity indices take into account the two main aspects of diversity – the number of species in a sample (generally referred to as S) and the distribution of individuals amongst those species. Hence such indices are influenced by how dominated the community is by certain species. Diversity indices have risen to prominence as they are frequently used to detect pollution. Pollution, such as organic enrichment, will often cause dominance by just one or two species, but there may be many other rare species present that have just happened to arrive by natural immigration. This dominance effect lowers the diversity index, even if the number of species does not change.

Two commonly used diversity indices are Simpson's index and the Shannon-Weaver index. Simpson's index is calculated by determining, for each species, the proportion of individuals that it represents in the sample, denoted as P_I or the proportion for the *i*th species. Rosenzweig (1995), citing Nei and Roychoudhury (1974) has demonstrated that a version of Simpson's index unbiased to sample-size can be calculated using the formula:

$$D = \Sigma ((n^2 - n) / (N^2 - N))$$

This is the formula used in this thesis, rather than the sometimes used:

$$D = \Sigma n^2/N^2$$

which is sensitive to sample size.

An alternative to Simpson's index is the Shannon-Weaver index, also calculated using an array of P_I values:

$$\text{Shannon - Weaver index } H = -\sum_{i=1}^{S} P_i \log_{10} P_i$$

Again, equitability itself can be calculated as the proportion of H over $H_{\max}$:

$$\text{Equitability } J = \frac{H}{H_{\max}} = \frac{-\sum_{i=1}^{S} P_i \log_{10} P_i}{\log_{10} S}$$

There has been considerable discussion on the relative merits of the different diversity indices. As a measure of diversity, H gives greater importance to the number of species while D gives greater importance to the equitability (Lambshead *et al.*, 1983). In this study, both indices are used. Also, the relative sample-size independence of D and H are investigated.

3.3.3 Rarefaction

The rarefaction methodology was invented by Sanders (1968) in his classic study of marine benthic diversity. The method works by randomly sub-sampling individuals from a population and using an algorithm (refined by Hurlbert (1971)) to determine the number of species for a set number of individuals. In this way, a 'number of individuals' independent measure of diversity can be ascertained. It is confusing to refer to rarefaction as a 'sample size' independent measure of diversity as the word sample could mean a set number of individuals, or a physical device, such as a box core. Rarefaction is in fact independent of sampling area *and* the number of individuals. The rarefaction algorithm generates a cumulative plot of the number of individuals on the x-axis, and the number of species for that number of individuals on the y-axis.

The y-axis figure is sometimes referred to as $E(S_n)$, or the expected number of species for n individuals. Although sample-size independent, rarefaction is highly influenced by equitability, especially at the low sample sizes common in the deep sea. In Figure 3.2A, the shaded area indicates the potential 'range' of diversity in a sample with 1600 individuals from 100 species. In Figure 3.2B, only the first 100 individuals have been selected, to simulate a deep-sea undersampling situation. In this hypothetical example, the three sites exhibit very different levels of diversity when measured at the n=100 level, even though they ultimately contain the same number of species (100). It is noticeable how the three curves in B appear, with a superficial glance, to differ in the number of species – it would be hard to imagine them ever meeting (even though the bottom one is a straight line). But in fact, as A shows, they all are derived from a sample with 100 species. This graph is derived from that shown in Gage and Tyler (1991) and Gage and May (1993).

Rarefaction has often been used as a measure of species richness (meaning the number of species) by several authors. But Gage and May (1993), Gray (1997) and Lambshead *et al.* (2000) have suggested that it is likely to be very sensitive to the equitability of a sample, as discussed above. A useful analogy might be made from a terrestrial system, where there is a much better idea of community boundaries and the true species richness. Imagine an oak tree in England and a fig tree in the Amazonian basin. Through extensive sampling, fogging experiments and so on, it is found that the oak tree has just 500 species of insect living on it, while the tropical fig has 5000 species. Sir Alister Hardy once suggested that marine sampling is equivalent to lowering a bucket from a balloon through a dense fog while floating over the study site. If this scenario is applied to this hypothetical terrestrial system then at the rich tropical site a teeming bucketful of thousands of insects would be expected, but at the oak tree maybe only 20 insects are discovered. The wildly different numbers of individuals between the

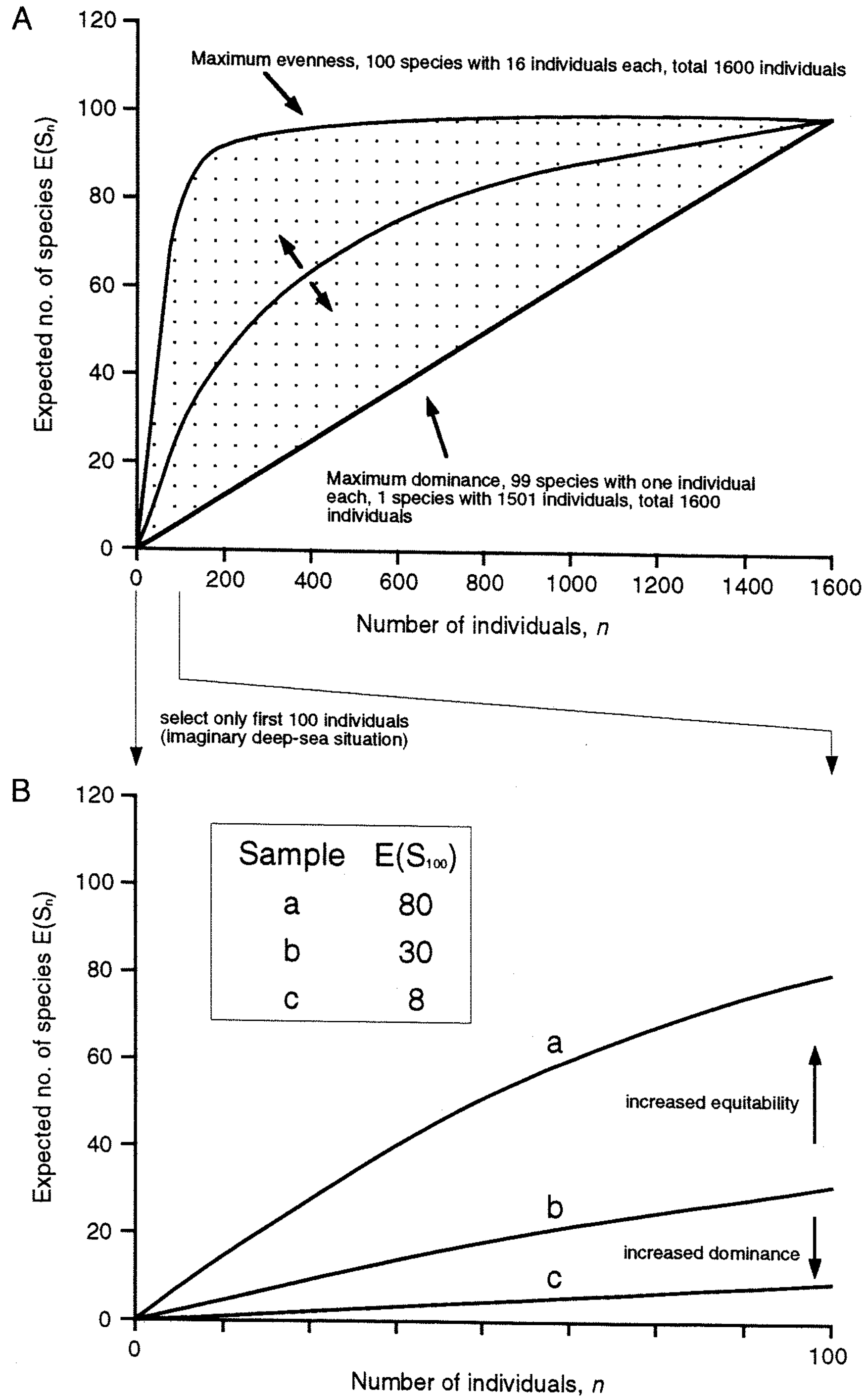

Figure 3.2 Rarefaction is highly influenced by equitability in this hypothetical example of a community of 1600 individuals and 100 species. The shaded area in A represents the potential range of diversity from the two extremes of maximum evenness and maximum dominance. In B, a deep-sea undersampling situation has been simulated where only the first 100 individuals have been sampled.

two sites might tempt the deep-sea biologist into using the sample-size independent measure of diversity – rarefaction. However, the sites can only be compared at a level of twenty individuals, obviously limiting the number of species to just twenty. Unless there was a very pronounced dominance effect then the diversity as measured by rarefaction would be the same. The point is, rarefaction in this case gives provides no clue as to species richness - just looking in the bucket would be more effective. At low E(S_n) values, rarefaction is also not very good at looking for differences in dominance either, as so much information is missing. The solution would be to drop some more buckets at the oak tree site to increase the number of individuals, at which point rarefaction would start to give you an indication of the relative evenness of the two samples, and also the position of the asymptote of the graph – a measure of species number.

Rarefaction is a useful way of comparing species diversity (i.e. a diversity index) when there are enough individuals to make it meaningful, and this is the approach adopted in this study. At very small sample sizes, spatial patterns of diversity break down (Rosenzweig, 1995). For this reason, box core diversities alone cannot be used as a measure of alpha diversity; the samples must be pooled in order to have enough individuals for meaningful comparisons to be made. In this study, rarefaction proved useful for comparing the abundant but sparsely sampled EqPac sites with the well sampled but impoverished manganese nodule sites.

3.3.4 Species accumulation curves

Gray (2000), while explaining the deficiencies of the rarefaction method, indicated an alternative method for generating a plot of estimated species number, using the *species accumulation curve* method. This method takes random samples and the number of species in each is plotted cumulatively. The advantage of this method is that it generates an estimated total number of species for the region that the samples lie in (i.e. alpha diversity if the samples are all within-habitat). However, Gray (2000) did not explain how such a method actually accounts for differences in density of individuals – even if it accounts for variations in sampling intensity. The species accumulation rate is indicative of beta diversity, or turnover diversity, and will only provide a reliable estimate of the true number of species when the curves begin to reach asymptote; this is rarely achieved in the deep sea. Species accumulation curves are calculated using 50 random sub-sampling repetitions.

A further method of evaluating the potential total number of species is the method of Chao (1987). This was used by Paterson *et al.* (1998) to estimate total species richness for the DOMES A site in the equatorial Pacific. An alternative is to evaluate whether species accumulation is related to area in log-log space (i.e. following the traditional species-area curve relationship described in section 2.3) and use the form of the species area equation to estimate total species richness for a given area.

3.3.5 Beta diversity

All the analyses of beta diversity (or faunal turnover), as well as the clustering methods, were performed using the program COMPAH96 (Gallagher, 1996). The simple index of Kulczynski (1927), expressed as a percentage, is a useful way of assessing the species turnover between sites. It relies only on the presence or absence of species and as such is less influenced by sample size. The index is given by:

$$1/2[s/(s+u) + s/(s+v)] \times 100$$

where s is the number of species common to A and B

u is the number of species found in A and absent in B

v is the number of species found in B and absent from A

The Kulczynski method can also be used to evaluate similarities between quantitative datasets, but for this study, the more flexible NESS method of Grassle and Smith (1976) has been used. NESS stands for Normalised Expected Species Shared. In COMPAH96, the NESS method of Grassle and Smith is modified so that it can properly analyse samples containing singleton species, this modified version is known as NNESS. The NNESS similarity measure is based on the number of species shared between random samples of fixed size m drawn from each population. In this sense it operates on the same principle as the rarefaction index – i.e. samples are randomly sub-sampled many times to generate an 'expected' level of similarity for a certain number of individuals, which forms the basis of the similarity measure, or the *expected species shared.* The advantage of the NNESS measure, as with the rarefaction measure, is the ability to alter the size of the sub-sample dependent on your data and the particular question you need to address. In COMPAH96, m can be altered from a value of 1 up to the size of the smallest population. At low levels of m, expected species shared is dependent on the dominant species; at high levels, the less abundant species will also contribute to the measure. At m=1, the NESS similarity measure is equivalent to the Morista-Horn absence/presence index.

3.3.6 Cluster analysis

The similarity measures described above generate a matrix of percentage similarities, which is somewhat difficult to interpret without further analysis. The normal method is to use a *combinatorial strategy* that works by joining together the two most similar sites, then adding the next most similar site and so on to produce a dendrogram or tree. COMPAH96 uses Lance and Williams' (1967) combinatorial equation:

$$d_{hk} = \alpha \times d_{hi} + \alpha \times d_{hj} + \beta \times d_{ij} + \gamma \times |d_{hi} - d_{hj}|$$

where, d_{hk} = distance between group h and fused group k, composed of i and j

d_{hi} = distance between groups h and i

d_{hj} = distance between groups h and j

α, β, γ = parameters set for specific sorting strategies

In COMPAH96 the parameters α, β, γ are altered to produce different sorting strategies. Many sorting strategies are incompatible with certain similarity indices. For example, the commonly used flexible average sorting method is incompatible with virtually all similarity or dissimilarity indices (Gallagher, 1996). This usually becomes apparent when the sorting strategy produces *negative* clustering levels, even when the similarity indices have 0 as a theoretical minimum. Jardine and Sibson (1968) reviewed the combinatorial strategies of Lance and Williams (1967) and concluded that only single-linkage clustering met their criteria for a valid clustering method. However, Williams (1971) suggested that there was scope for a certain 'relaxing' of these criteria and that the average clustering strategies could be used. In this study, both single-linkage and the more commonly used group-average methods are used. As with most statistics, a disagreement between the results would tend to indicate that the data are inconclusive, rather than that the chosen clustering algorithm is the wrong one.

3.3.7 Ecological cladistics

Ecological cladistics has been proposed as an alternative to the more traditional multivariate similarity techniques (Lambshead and Paterson, 1986; Legendre, 1986; Bellansantini *et al.*, 1994; Glover *et al.*, 2001). Its origins and use are discussed here in some detail as it is a new and rarely used ecological multivariate technique.

The method is adapted from the numerical methodology used to reconstruct phylogeny, or cladistics. The methods and terminology of cladistics were developed by Willi Hennig in the mid 1960s (Hennig, 1966). The guiding principle of cladistics is the identification of shared, derived characters, or *synapomorphies*, which are characters that define a clade. The branchial crown of sabellid polychaetes would be a good example of a synapomorphic character. Synapomorphies are distinguished from uninformative *autapomorphies* which are characters that are only present in one species (i.e. they define the species by being present in all the individuals of that species). Upright walking in *Homo sapiens* could be considered an autapomorphy – it is a useful species specific character but is not informative regarding the relationship between humans and other apes. At the other extreme, *plesiomorphic* characters are those that are present in all of the taxa in the analysis. The universal genetic code would be the ultimate example of a plesiomorphic character – again not useful for elucidating the relationships between humans and apes. Cladistics is only concerned with shared, derived characters, not differences between species. This is because cladistics is about reconstructing phylogeny, or the evolutionary tree of life. Cladistics is abductive inference of a past process based on the observed patterns of characters we see today. Within those patterns of characters are the remnants of evolutionary history, the synapomorphic characters. The cladistic methodology uses only these characters to group species.

The problems and controversy in cladistics lie in identifying the synapomorphic characters. This is because some characters may be shared between species but not actually be ancestral to both. These are the analogous characters, of which one example might be the presence of a wing in both birds and bats. Most cladists get around this problem by using the principle of maximum parsimony to evaluate their cladograms. The most parsimonious route is the shortest and quickest route. In the bird and bat wing example, there are many good synapomorphic characters that support the hypothesis that birds and bats are from separate clades, and that the presence of a wing is a *homoplastic* character – i.e. it has evolved twice on the tree. The point is, it would be much less parsimonious to say that the presence of the wing is the synapomorphic character and the hundreds of other characters are all homoplasies. In terms of evolutionary steps, the tree would be much longer.

It is not known how parsimonious nature is. This is undoubtedly the single most controversial issue in cladistic theory. No one would doubt that there is a certain degree of parsimony in nature – humans did not evolve from monkeys by way of a geranium. But is maximising parsimony always going to give the correct result? This issue has dogged the often surprisingly vicious debate in the cladistic literature. Many scientists have thought of parsimony as an assumption about the way evolution works. For this reason it has been heavily criticised and many have gone back to using statistical similarity measures such as the 'maximum likelihood' measure. But J S Farris, in his seminal paper (1983) outlined why parsimony is not actually an assumption, it is simply choosing the hypothesis with the most explanatory power. Take three taxa, A, B and C where there are 10 putative synapomorphies for A + B and just one for B + C. In this case, the most parsimonious grouping is ((A, B) C). So, if homoplasy is indeed rare then this is likely to be the correct tree. The question is, what increase in the degree of homoplasy is necessary to upset this relationship? Or, in other words, does a change in the amount of parsimony in evolution make any difference to the hypothesis? It is clearly apparent that for a different tree to be selected, i.e. ((B, C) A), requires that all 10 of the A + B synapomorphies actually be homoplasies. If the characters are all independent then this is clearly statistically improbable. Imagine also a situation where homoplasy is very abundant and only one of the characters is not homoplastic. It could equally be any one of the 11 characters, and the fact that ten of the characters are present in A + B means that 10 times out of 11 the ((A, B) C) tree will be the best bet. In the very extreme, where homoplasy is universal, then none of the characters are informative about evolution and the most parsimonious grouping will be no better founded than any other, but then neither will it be any worse founded. Farris (1983) summed up this thinking:

> *"It seems that no degree of abundance of homoplasy is by itself sufficient to defend the choice of a less parsimonious genealogy over a more parsimonious one. That abundance can diminish only the strength of preference for the parsimonious arrangement; it can never shift the preference to a different scheme. In this the relationship of abundance of homoplasy to choice of genealogical hypothesis is quite like that between residual variance and choice of regression line. Large residual variance expands the confidence interval about the line, or weakens the degree to which the least squares line is to be preferred over nearby lines, but it cannot by itself lead to selection of some other line that fits the data even worse."*

The analogy with the regression line is a particularly valid one, and is useful in explaining why cladistics has a use in ecological analysis. The point is, there is nothing inherently 'special' about using the principle of parsimony. There are no assumptions about the process of evolution, it is simply a way of maximising the explanatory power of the data - in just the same way as a regression line through a spread of ecological data. Of course the usual caveats must apply – just as with a positive regression, cause and effect cannot be known, but then neither can it be certain that a genealogy has actually been created by evolution. In ecology, more measurements, or an experiment would be required. The systematist would need to check the fossil record, or analyse the molecular data. In philosophical terms, the ecologist is doing the same thing as the cladist – abductive inference.

If parsimony is doing no more than putting a 'best fit' on our data, it is easy to see how it may be useful in the analysis of species assemblages. The small methodological jump that is needed is to treat what would have been the terminal taxa in a phylogenetic analysis (often, but not always, species) as sites. In the same way, the characters of a phylogenetic analysis become the species in an ecological one.

For this study, species by site matrices were analysed using the program PAUP 3, standing for Phylogenetic Analysis Using Parsimony (Swofford, 1993). In PAUP, the default option is for *reversible* unordered characters (the Wagner algorithm), as this is the option with the least assumptions about the data – in fact it makes no assumptions at all. The thinking behind this is that in evolutionary terms, it is likely that characters are equally likely to be lost as they are to be gained. Lambshead and Paterson (1986) have suggested that for ecological analysis, it is valid to make the assumption that species are not 'lost' from sites. Hence in terms of the PAUP analysis, it is important that the species (or characters, in a phylogenetic sense) are made *irreversible*, that is, only 0 → 1 is permitted, not 1 → 0. This is sometimes known as the Camin-Sokal method. Sites are thus only grouped on the shared presence's of species, not their 'derived' absences. This is because the absence of a species from a site could be due other factors, such as inadequate sampling.

For a given number of sites, it is possible to calculate the maximum number of tree rearrangements. With 4 sites, there are just 15 possible rearrangements. With 5, there are 105 and with 20 there are 2×10^6. PAUP works by calculating the number of steps (species transformations) on each tree and selecting the tree with the shortest length. PAUP can analyse millions of trees in minutes, but even so it is sometimes necessary to adopt a 'heuristic' search pattern. The program generates a frequency distribution of tree lengths and 'jumps in' at randomly selected points along this distribution, saving any short trees as it goes. If enough random searches are conducted, the shortest trees are normally found without actually needing to search every tree. Where more than one tree was discovered, a consensus tree was generated – these are most useful for examining which sites are inconsistent between trees and could potentially be excluded. If all the most parsimonious trees are very similar then this is reflected in a consensus tree with good resolution. If all the trees are very different then the consensus tree is normally collapsed.

The use of parsimony in ecology has a number of advantages over other multivariate techniques. The first is that when the data are inconclusive, no resolution is normally obtained in the consensus trees. PAUP does not always produce a result, whereas a clustering algorithm will *always* force the data to cluster somehow. The second advantage is that it is a one-stage analysis. In other multivariate techniques, first a percentage similarity is calculated, then a clustering algorithm is applied to the similarity matrix. There are numerous examples in the literature where incompatible clustering algorithms have been applied, and the relative merits of different clustering algorithms is still under debate. In PAUP, the geographical spread of the species is evaluated directly and a 'best fit' produced, just as in a regression analysis. PAUP also allows for an estimate of tree support, in terms of the consistency index (CI), retention index (RI) and other statistical methods such as bootstrap. The tree can be altered graphically to indicate the branch support – i.e. the number of species that each node represents. Using the program MacClade (Maddison and Maddison, 1997), the position of species on each node can be plotted graphically, and the trees manipulated over a map for enhanced visual impact. Several authors have already used parsimony in ecological analysis and found it to be successful (Lambshead and Paterson, 1986; Legendre, 1986; Bellansantini *et al.*, 1994; Glover *et al.*, 2001).

One disadvantage is that it is not so easy to incorporate quantitative data in the analysis. In this study, a way round this was found by calculating the percentage contribution (in terms of individuals) of the synapomorphic species and plotting these as cumulative box plots overlaid on the graph. In this way the numerical importance of the cosmopolitan and the unique species could be elucidated. One other potential way of including quantitative data would be to artificially weight the species (characters in PAUP) using the character-weighting option, although this was not done in this study.

4 TAXONOMY

> *"None but a naturalist can understand the intense excitement I experienced when at last I captured it [a new species of butterfly]. My heart began to beat violently, the blood rushed to my head, and I felt much more like fainting than I have done when in apprehension of immediate death. I had a headache the rest of the day, so great was the excitement produced by what will appear to most people a very inadequate cause."*
>
> *- Alfred Russell Wallace (1908)*

4.1 Introduction

The purpose of this chapter is to outline the taxonomic method employed and to illustrate two contrasting examples of abyssal polychaete taxonomy. It can be viewed as both a methodological (the method of generating the data for chapter 6) and results (alpha taxonomy in its own right) chapter.

Taxonomy is the science of classifying organisms. Human civilisations arose through increasing taxonomic knowledge of the environment and the ability to classify and order a chaotic world. At first it was easy. Large organisms fell naturally into related groups; within those groups discrete clusters of near-identical individuals were apparent. This morphological pattern was the result of the processes of evolution, speciation and sexual reproduction, although at the time, the early taxonomists did not know this. The species concept and the idea of a 'hierarchy' of relatedness was first developed on a large scale by the Swedish naturalist Linnaeus (Linné, 1758). The early taxonomists concentrated on the larger organisms within the spatial scale of our own existence, or those organisms that are of use to us. Nowadays, most new species are very small and come from unexplored areas of the rainforest or the deep sea. Quite recent quantitative studies from these areas have shown that the taxonomists should not be out of work for quite a long time yet. Grassle and Maciolek (1992) suggested that there may be over ten million deep-sea macrofaunal species waiting to be described. Erwin (1982) calculated that there are likely to be at least 30 million arthropod species.

Of those ten million deep-sea macrofaunal species, probably about 60% are polychaetes. That is six million deep-sea polychaete species. Only a few hundred have been described. Only one abyssal polychaete has been described in the past few years (Paterson and Glover, in press). This completely insurmountable problem has led to a change in the attitude of taxonomists. No longer is it expected that a complete inventory of life on the planet will be created. Rather, species that are to be described must have some 'added value' in terms of their ecological, functional or evolutionary significance. The one abyssal polychaete described in the last few years was interesting in that it was very abundant, predatory and present throughout the north Atlantic. Hence it is a reasonable candidate for a species of ecological significance, and one that would certainly be found by other workers were they to go looking in the same place. Probably the next step for deep-sea polychaete ecology is to investigate reproductive biology – for this to happen at least *some* described species are needed.

Taxonomy is under attack from other directions too. This debate is probably too wide to go into in detail, but must at least be discussed. Ecologists would be foolish to ignore a revolution in the main theoretical underpinning of the biological sciences – the classification of life. Very recently, there has been a surge of interest in a new system of classification, known as phylogenetic taxonomy (de Queiroz and Gauthier, 1992; de Queiroz and Gauthier, 1994; Sundberg and Pleijel, 1994; Schander and Thollesson, 1995; Mishler, 1999; Pleijel, 1999; Pleijel and Rouse, 2000). The reason for this revolution is as follows. Traditional Linnean taxonomy is based on a non-evolutionary view of the world; Linnean ranks such as family or class are groups that for subjective reasons have been given greater prominence and a *rank* in the hierarchy. There are three reasons why this has caused problems. The first is that having a classification system based on the subjective ideas of individual taxonomists goes against scientific principles. Building classification systems without theoretical underpinning is what biologists have been doing for centuries. Mainly this is because there has not been a sound theoretical underpinning. But this is no longer the case, there are the theories of evolution and population genetics, which should form the basis of such classifications. The second reason is that because most aspects of the zoological code revolve around the rank, when a change in relationships is discovered several names have to be adjusted. Unnecessary changes of names also occur when the rank of a group is moved without its relationships being altered. The final reason is that the Linnean system is often assumed by ecologists and others as being of use for comparative purposes. While there is no doubt that many of the ranks represent valid monophyletic groups (most of the polychaete families, for example) it is wrong to suggest that one rank is equivalent to another. Ecologists may frequently use Linnean ranks as erroneous measurements of biodiversity – by counting the number of taxa at a particular rank, for example.

The main point is that those in favour of phylogenetic classification do not intend to get rid of a hierarchical system. Evolution provides a natural hierarchy in the form of nested groups. But in phylogenetic taxonomy, it is the series of nested groups that are important, and there are no ranks attached to them. Phylogenetic taxonomy encourages stability in clade names by preventing needless changes associated with movements of rank. Polychaetes (assuming they are monophyletic) will always be polychaetes, even if it turns out that the group is a much more all encompassing clade than previously thought. The new system is not yet completely formulated, but a new Phylogenetic Code of Nomenclature is currently being drawn up. The current version, published at present on the internet[6], consists of a system of nested uninomials

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[6] http://www.ohiou.edu/phylocode/index.html

based on currently accepted cladograms. It seems probable that for a time, there will be a split between journals that accept the new phylogenetic taxonomy and those that do not.

Phylogenetic taxonomy is certainly not universally supported (Dominguez and Wheeler, 1997; Liden *et al.*, 1997; Moore, 1998). There are a number of powerful arguments against it, namely that: (1) changing to a new system of nomenclature will be difficult and confusing for many workers who use the Linnean system for ecological or other analyses, (2) the uninomial system raises the problem of homonymy – i.e. where the species name is used more than once there will have to be some way of recognising the clade (formerly genera) that it belongs to, and this will in effect, require the reinstatement of a binomial and finally (3) some authors point out that the Linnean system is not necessarily incompatible with phylogenies, so long as the emphasis on the equivalence of ranks is removed.

There is no doubt that transferring to a new system will be difficult. But if the current system is unsatisfactory then continuing to use that system will also be 'difficult'. Politicians who come to power do not, one hopes, ignore poverty and unemployment just because they are intractable issues. Having said that, many of the problems with the Linnean system stem from the general inadequacy of historical descriptions, the lack of supporting morphological/molecular evidence and the general shortage of taxonomists. Were these problems to be removed, so would many of the problems with the Linnean system. Whilst there is no doubt that a classification system should be based on evolutionary theory (and the vast majority of taxonomists now hold this view), it must also be useful for people studying the patterns and processes of the natural world. There is no doubt that the use of the Linnean system is severely restricted by its limited design, and that it encourages 'bad science'. On the other hand, the uninomial system also has a number of practical disadvantages, not least of which will be the difficulty in transferring to it.

This very brief review was intended to highlight the exciting position that the science of taxonomy stands today. The taxonomic work in this thesis was principally intended to determine diversity, and hence most species have not been named beyond being given a unique number. In some ways, it may be best to leave it there until the taxonomists have finished arguing. For deep-sea species, phylogenetic taxonomy may well be a useful advance. This is not because there are well resolved cladograms for deep-sea groups, rather, completely the opposite. Where clades are unresolved, phylogenetic taxonomy adapts. If no monophyletic genera can be resolved using the current data, phylogenetic taxonomy would simply ignore what would have been genera, until such time that better data are available. The next available monophyletic node is used instead. There is no attempt to 'shoehorn' species into genera where no such data are available.

In the following sections, two different approaches to deep-sea taxonomy are illustrated. In section 4.2, a review of the cirratulid polychaetes from the EqPac sites, the approach for a difficult and unknown fauna is outlined. In this, unique numbers are assigned to descriptions of morphological groupings of individuals (in effect, *clades* of individuals) that form the putative species. A key has been generated and the characters are discussed. In section 4.3, a more formal Linnean approach has been used in the description of a new species of *Sigambra* (Pilargidae) from the north-east Atlantic sites.

4.2 Cirratulidae from the Abyssal Plains of the Central Equatorial Pacific

4.2.1 Introduction

The purpose of this section is to highlight the taxonomic approach for a 'difficult' group, the cirratulids, and to indicate how 'clades' of individuals are identified and assigned to putative species groups. It is on these species groups that subsequent analyses of diversity rest.

Cirratulids are small to medium-sized polychaetes well known from shallow water where they may live in the sediments, rock crevices or amongst seagrasses and algal holdfasts (Glasby, 2000). The family was first erected by Carus, Peters and Gerstäcker (1863). They are characterised by a conical or anteriorly rounded prostomium lacking appendages and a peristomial region with at least two fused segments. Palps may be as paired grooved tentacles as in *Dodecaceria* or as multiple filaments arising from anterior chaetigers as in *Cirriformia*. Parapodia are biramous with simple chaetae that may form capillaries, hooks or acicular spines. Paired, slender branchial filaments arise from the dorsal surface of each segment.

Since the erection of the family, a number of systematic reviews have taken place (Carus and Gerstacher, 1863; Grube, 1872; Caullery and Mesnil, 1898; Hartman, 1961; Blake, 1991). Blake (1991) reviewed species from the western north Atlantic, redefining the genus *Tharyx*, erecting a new genus *Aphelochaeta* and resurrecting an old genus *Monticellina*. But a large number of systematic problems remain, and in particular the monophyly of certain genera is certainly in question (Glasby, 2000).

Deep-sea cirratulids are common; in the north-east Atlantic they may represent up to 20-30% of the total number of individuals (Glover *et al.*, 2001). The most abundant genera are *Chaetozone*, *Tharyx* and *Aphelochaeta*. *Caulleriella* and *Monticellina* have also been recorded from bathyal depths. Like many deep-sea groups, they are reduced in body size compared to their shallow-water relatives. At the EqPac sites, they ranged from 1.6 to 5.2 mm in length, although the great majority of specimens fragment and only the head fragments are available. In contrast, some shallow-water cirratulids have been known to reach 250 mm in length. For fragmented animals, body size was estimated by measuring the width of the animal and the length of the first ten chaetigers.

In common with other deep-sea polychaetes, the cirratulids show a tendency for 'character loss'. Many of the morphological modifications and adaptations of shallow-water genera are reduced or absent in deep-sea forms. This makes the taxonomy more difficult, and in this case, new characters had to be found in order for morphological groupings (from hereon termed 'species') to be made. In particular, the absence of the abdominal section for many specimens was a problem; the presence, position and nature of abdominal acicular spines is an important generic and specific character for *Chaetozone*, *Tharyx* and *Aphelochaeta.*

For these reasons, new characters based on the shape and relative sizes of various features associated with the thoracic region have been developed. Characters based on shape are problematic owing to the potential for the observer's own subjective whims as to what is round and what is pointed and so on. A pictorial description of these 'shape' characters is provided in the following section, which goes someway to alleviating this problem. Nevertheless, it is clear that more unfragmented material is needed to strengthen these species groupings.

A problem arises with the assignment of generic groupings for a number of these species. This is because certain abdominal generic characters could not be observed. Following the premise of phylogenetic taxonomy, only monophyletic nodes are supported – hence where there is insufficient information for a sub-familial clade grouping to be made, only the family and species number is given.

The methods of collection are described in section 3.1.2. All specimens were collected using the spade box core.

4.2.2 Discussion of characters

In the following section, the code letters for each character refer to the columns in the tabular key (Table 4.1). Note that all measurements of body position refer to the chaetiger number, not the segment number and that the measurements of relative length use the width of the chaetigers in the anterior portion of the thoracic region as a standard unit.

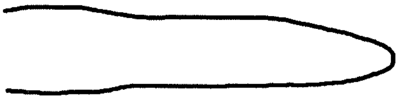
Thoracic Body Shape (TBS): It was noted that a number of species exhibited characteristic thoracic body shapes, with different regions of the body swollen or enlarged. Although this appeared to be a species character, it is possible that it may be an artifact of fixation or associated with asexual modes of reproduction, and as such should be treated cautiously.

0: Uniform width throughout

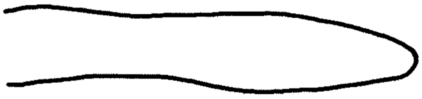
1: Swollen anterior end (just below peristomium)

2: Swollen mid region

3: Swollen posterior region



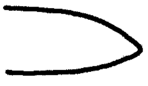
4: 'Hour-glass' shaped



Prostomium shape (PRO): The prostomium shape is a useful character for species recognition in cirratulids. In this case, three further subdivisions of the 'pointed' group can be made, differing in the position and nature of the narrowing of the prostomium. In certain specimens, the prostomium would start to narrow from the peristomial region onwards ('tapering prostomium'), in others the narrowing would only occur at the very tip, giving a 'snout-like' appearance. In some the narrowing was between these two extremes, or 'conical'.

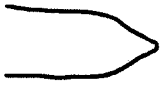
0: Rounded

1: Pointed, conical



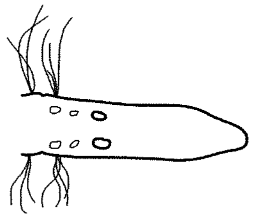
2: Pointed, conical, tapering from peristomium

3: Pointed, snout-like

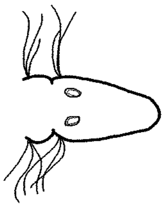


Buccal region (BR): The buccal region in this sense is the peristomial region, including the fused segments. In some species this was elongated to greater than 4 chaetigers in length, in others it was less than 2 chaetigers in length (compact).

0: Elongate

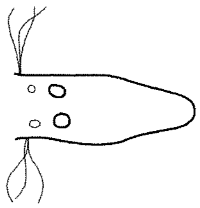


1: Compact

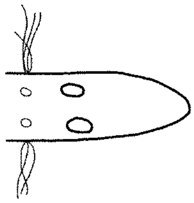


Palps (PALPS): The position of the palps with respect to the first chaetiger was categorised on the basis of the number of 'branchial widths' – i.e. the diameter of the branchial scar – between the palps and the first chaetiger.

0: Less than 2 branchial widths to ch. 1



1: More than 2 branchial widths to ch. 1



Very long ('bottle-brush') chaetae (BBC): The 'bottle-brush' chaetae are those capillary chaetae that are greater than 5 chaetigers in length. In some specimens they are so long as to form hair-like 'tangles' around the specimen.

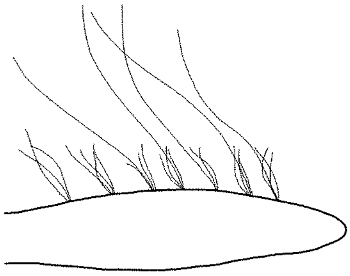
0: Absent

1: Present

Thoracic bottle-brush chaetae (TBBC): The position of the first appearance of the bottle-brush chaetae is a useful species specific character.

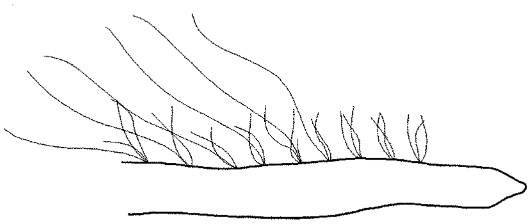
0: Absent

1: From chaetiger 1



2: From chaetiger 2

3: From chaetiger 4



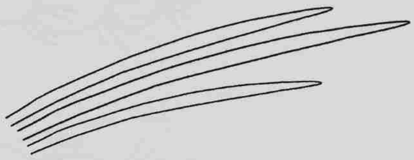
4: From chaetiger 5

5: From chaetiger 6 or 7

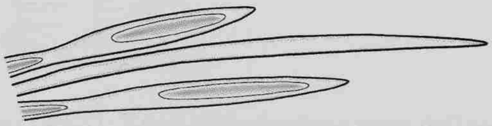
6: From chaetiger 9

Thoracic neurochaetae (TNEUR): Thoracic neurochaetae are of two types – simple short capillaries (from hereon termed 'simple capillaries') and stout acicular spines (from hereon termed 'acicular spines')

0: All simple capillaries



1: Acicular spines present



Thoracic acicular spines (TAS): The position of the thoracic neurochaetal acicular spines is a species specific character.

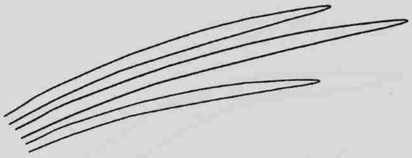
0: Absent

1: Begin on chaetiger 1

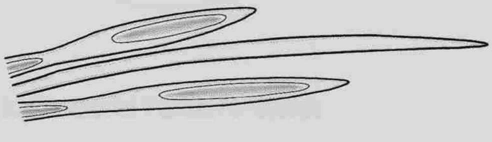
2: Begin on chaetiger 7

Abdominal acicular spines (AAS):

0: Absent

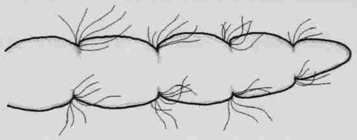


1: Present

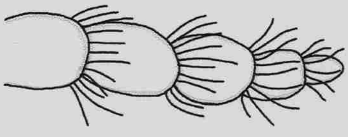


Abdominal cinctures (AC): In some specimens, complete 'cinctures' of alternating acicular spines and capillaries would be present in the abdominal region.

0: Absent

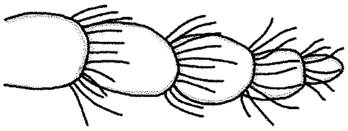


1: Present

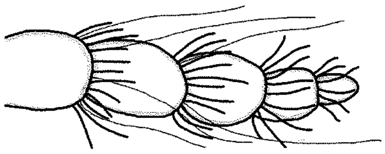


Abdominal bottle-brush chaetae (ABBC): In some specimens, bottle-brush chaetae were present in the abdominal region.

0: Absent



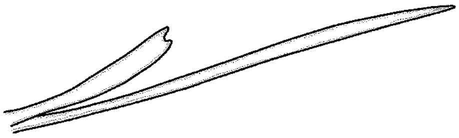
1: Present



Abdominal knob-tipped spines (AKS): Knob-tipped spines were defined by Blake (1991) for the genera *Tharyx*.

0: Absent

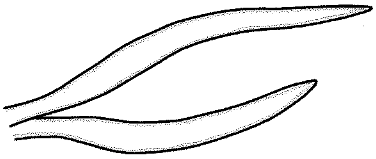
1: Present



Abdominal 'banana' shaped spines (BANS): These uniquely-shaped spines were found in the abdominal region of some specimens.

0: Absent

1: Present



4.2.3 Key to Equatorial Pacific cirratulids

This is a multi-access tabular key designed to be used in conjunction with the discussion of characters above. Tabular keys have the major advantage over traditional dichotomous keys in that ambiguous characters can be excluded without limiting the use of the key. This is especially useful where characters based on subtle changes in shape are used, as is the case here. In addition, they are suitable for use in cladistic analysis programs such as PAUP.

	TBS	PRO	BR	PALPS	BBC	TBBC	TNEUR	TAS	AAS	AC	ABBC	AKS	BANS
sp. 810	0	1	0	0	1	6	1	1	?	?	?	?	?
sp. 824	2	0	0	0	1	5	1	2	?	?	?	?	?
sp. 812	1	3	?	1	1	5	1	2	?	?	?	?	?
sp. 828	2	2	1	0	1	1	0	0	1	1	1	0	0
sp. 827	0	2	1	1	1	2	0	0	1	?	?	0	0
sp. 814	0	2	0	0	0	0	0	0	1	0	0	0	1
sp. 815	1	?	?	?	1	5	0	0	1	0	0	0	1
sp. 811	1	2	0	0	0	0	0	0	?	?	?	?	?
sp. 816	2	3	0	0	0	0	0	0	?	?	?	?	?
sp. 818	1	2	1	1	1	3	0	0	?	?	?	?	?
sp. 829	3	3	0	0	1	4	0	0	?	?	?	?	?
sp. 831	0	0	0	1	1	2	0	0	?	0	?	0	0
sp. 823	4	1	0	0	1	1	0	0	?	?	?	?	?
sp. 817	0	1	0	1	1	6	0	0	?	?	?	?	?
sp. 820	1	2	0	0	1	3	0	0	?	?	?	?	?
sp. 832	0	1	1	?	0	0	0	0	1	0	0	1	?
sp. 836	2	1	0	1	1	2	0	0	1	1	0	1	?
sp. 819	2	3	0	0	1	3	0	0	1	1	0	1	1

Table 4.1 Character matrix. See pictorial key above for character code explanation. Group A (black), Group B (green), Group C (red), Group D (blue), Group E (purple) (see text for explanation).

4.2.4 Analysis

The phylogenetic analysis program PAUP 3 (Swofford, 1993) was used to investigate whether the species could be grouped on the basis of parsimony. No most parsimonious arrangement could be produced using the character matrix in Table 4.1. Over 1500 shortest trees were generated; large differences between them indicated that most of the characters exhibit a high degree of homoplasy. This was not a surprising result given the nature of the characters investigated; characters of shape and size are unlikely to be of use as potential homologies, but in this case they are useful as potential species identifiers. Further work on full character sets using a variety of both deep and shallow-water taxa would be required before potential sub-familial clades are to be identified.

In the following descriptions, some groupings have been identified for practical purposes alone (Table 4.1). The large number of species makes comparisons between them difficult without first identifying some general groupings. It should be stressed that the data are not good enough to suggest whether species conform to particular established genera, or whether new genera would have to be erected, were this analysis to use the traditional Linnean system. Where certain species appear morphologically close to established genera, this has been indicated.

4.2.5 Group A – 'thoracic acicular spine group'

Diagnosis: Stout acicular spines in the thoracic region, starting at either chaetiger 1 or chaetiger 6.

Sp. 810

7 individuals examined. (BC#5 0°N 1-5cm EP001; BC#16 5°N 1-5cm EP033; BC#9 2°N 1-5cm EP035; BC#12 2°N 1-5cm EP041; BC#06 0°N 1-5cm EP051; BC#15 5°N 1-5cm EP083; BC#08 0°N 1-5cm EP103)

Description: Thoracic body shape of uniform width throughout. Prostomium pointed, conical. Peristomial region narrower than prostomium, elongated buccal region. Palps less than 2 branchial widths to chaetiger 1. Branchial scars visible on all thoracic chaetigers.

Thoracic notochaetae from chaetigers 1 to 8 are short simple capillaries approx. 1 chaetiger length and longer simple capillaries approx. 3 chaetigers in length, from chaetiger 9 very long 'bottle-brush' capillary chaetae > 6 chaetigers in length are present. Thoracic neurochaetae are 1-2 stout acicular spines, each spine with accompanying short simple capillary

Remarks: This species does not fit any established cirratulid genus, owing to the presence of acicular spines from the first thoracic neuropodia. Note that these spines differ from those often present in the abdominal sections of *Chaetozone* in that they do not show a concave region just below the tip - rather they are more rounded or convex.

Habitat: Central equatorial Pacific, 4300 m 0°N 140°W to 4400 m 5°N 140°W. This species was found exclusively within the sediment at a depth of 1-5 cm.

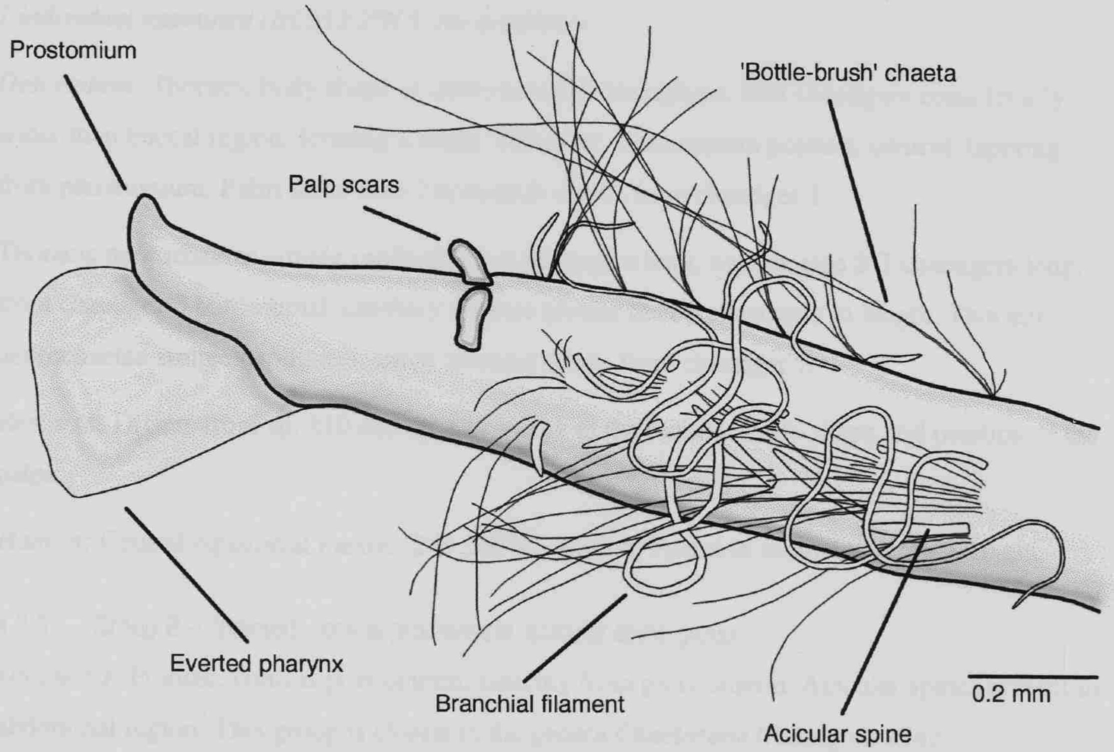


Figure 4.1 Cirratulid sp. 810. Stout acicular spines are present in the notopodia from the 1st chaetiger; pharynx partially everted.

Sp. 824

4 individuals examined (BC#16 5°N 1-5cm EP032; BC#15 5°N 1-5cm EP085; BC#10 2°N 1-5cm EP043; BC#15 5°N 1-5cm EP078)

Description: Thoracic body shape slightly swollen in mid-region (chaetigers 10-22). Prostomium rounded. Buccal region elongate, not noticeably narrower than prostomium. Palps less than one branchial width to first chaetiger. Branchial scars evident, becoming indistinct at chaetiger 10. Branchial scars sited approximately 2 branchial widths dorsal to notopodia.

Thoracic notochaetae from chaetigers 1-6 are short simple capillaries of 1 chaetiger length and longer simple capillaries of 3-4 chaetiger lengths, from chaetiger 7, bottle-brush capillary chaetae of length greater than 9 chaetigers appear forming hair-like 'tangles' around the body of the animal. Thoracic neurochaetae are simple capillaries of 2 chaetiger lengths, from chaetiger 7 stout acicular spines present.

Remarks: Differs from sp. 810 in the shape of the prostomium and the position of the acicular spines in the thoracic region.

Habitat: Central equatorial Pacific from 2°N 140°W 4400m to 5°N 140°W, 4400m, exclusively within the 1-5 cm sediment layer.

Sp. 812

1 individual examined (BC#12 2°N 5-10cm EP003)

Description: Thoracic body shape of uniform width throughout, first chaetigers considerably wider than buccal region, forming a slight 'shoulder'. Prostomium pointed, conical, tapering from peristomium. Palps more than 2 branchial widths from chaetiger 1.

Thoracic neurochaetae simple capillaries 1-2 chaetigers long, notochaetae 2-3 chaetigers long, from chaetiger 6 bottle-brush capillary chaetae greater than 5 chaetigers in length. Thoracic neurochaetae simple capillaries, small acicular spines from chaetiger 7.

Remarks: Differs from sp. 810 and sp. 824 owing to the thoracic body shape and position of the palps.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m. Found in sediment depth 5-10 cm.

4.2.6 Group B – 'pointed, conical prostomium, acicular spine group'

Diagnosis: Pointed, conical prostomium, tapering from peristomium. Acicular spines present in abdominal region. This group is closest to the genera *Chaetozone* Malmgren 1867.

Sp. 828

4 individuals examined (BC#6 0°N 0-1cm EP064; BC#6 0°N 0-1cm EP069; BC#5 0°N 0-1cm EP 004; BC#9 2°N 0-1cm EP021)

Description: Thoracic region swollen in mid region (chaetigers 6-11). Prostomium pointed, conical, tapering to a point. Buccal region compact. Palps less than two branchial widths from chaetiger 1.

Thoracic notochaetae short capillaries 2-3 chaetigers in length, bottle-brush capillaries greater than 5 chaetigers in length from chaetiger 1. Thoracic neurochaetae short capillaries of 2-3 chaetigers in length. Intermediary body region between thorax and abdomen present (Figure 4.2) of short capillaries 1 chaetiger in length. Moniliform abdominal region from chaetigers 18-32 with long bottle-brush chaetae, acicular spines forming complete cinctures composed of two types of chaetae - alternating thick acicular spines and slightly longer simple capillary chaetae (Figure 4.2).

Habitat: Central equatorial Pacific, 0ºN 140ºW, 4300m to 2ºN 140ºW 4400m. Present only in the 0-1 cm sediment layer.

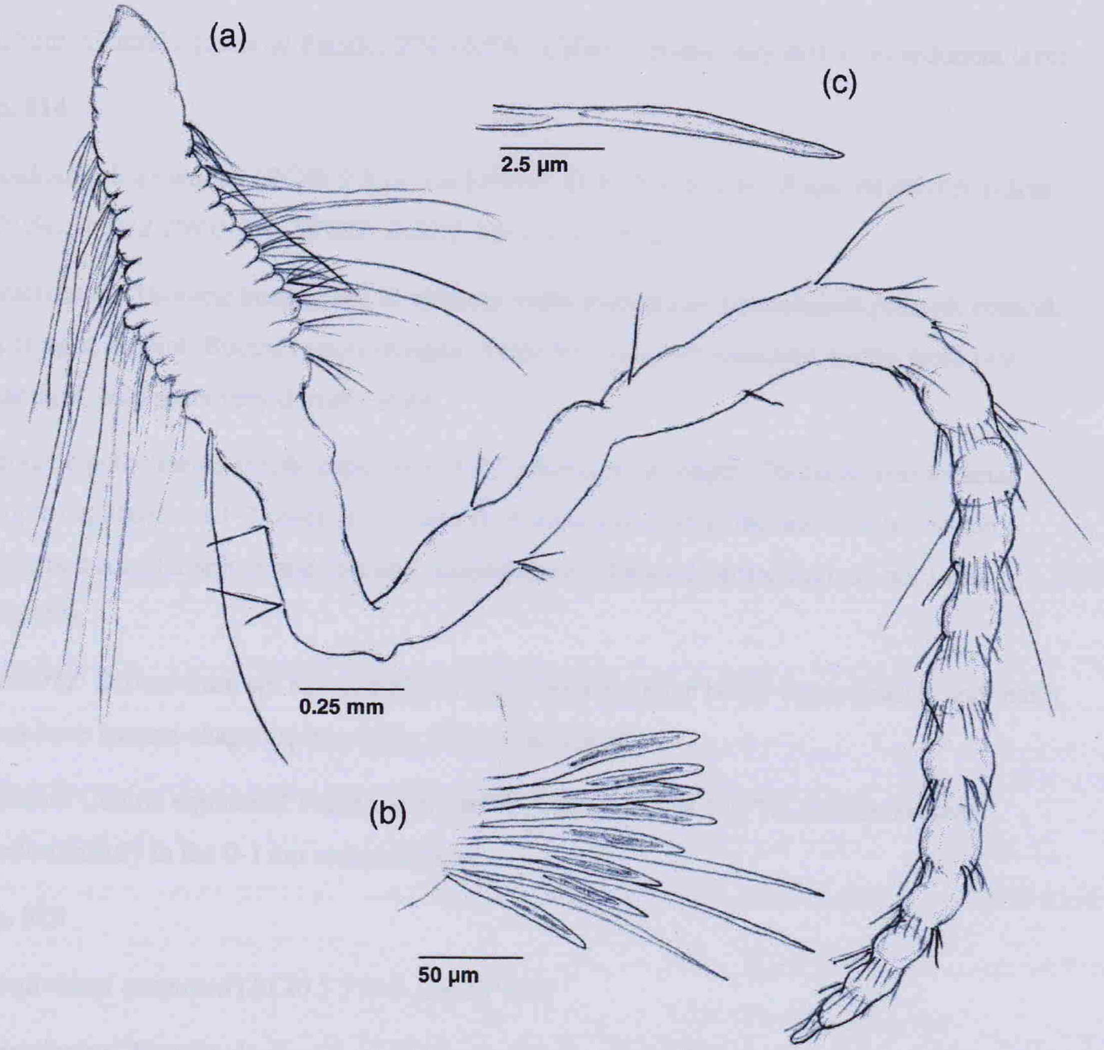


Figure 4.2 Sp. 828. (a) view of entire body; (b) arrangement of spines in posterior chaetigers; (c) detail of acicular spine.

Sp. 827

3 individuals examined (BC#6 0°N 0-1cm EP065; BC#8 0°N 0-1cm EP055; BC#8 0°N 0-1cm EP062).

Description: Thoracic body shape of uniform width throughout. Prostomium pointed, conical, tapering from peristomium. Buccal region compact. Palps sited more than two branchial widths forward of first chaetiger.

Thoracic notochaetae simple capillaries of 2-3 chaetigers in length, from chaetiger 2 very long bottle-brush capillaries appear greater than 5 chaetigers in length. Thoracic neurochaetae simple capillaries no more than 2-3 chaetigers in length. Abdominal acicular spines observed in fragmented abdominal region of some specimens, precise arrangement not observed.

Remarks: Differs from sp. 828 in terms of the position of the palps, and the starting position of the bottle-brush chaetae (on ch. 2 rather than ch. 1).

Habitat: Central equatorial Pacific, 0°N 140°W, 4300m. Present only in 0-1 cm sediment layer.

Sp. 814

5 individuals examined (BC#6 0°N 0-1cm EP073; BC#5 0°N 0-1cm EP006; BC#6 0°N 1-5cm EP054; BC#12 2°N 0-1cm EP029; BC#15 5°N 0-1cm EP109)

Description: Thoracic body shape of uniform width throughout. Prostomium pointed, conical, tapering to a point. Buccal region elongate. Palps less than two branchial widths from first chaetiger, palp scars very dorsally sited.

Thoracic notochaetae simple capillaries of 2-3 chaetigers in length. Thoracic neurochaetae simple capillaries of 1-2 chaetigers in length. Abdominal chaetae include simple chaetae, thickened acicular spines and 'banana' shaped spines (forward-projecting), do not form cinctures.

Remarks: Differs from sp. 828 and 827 in that it does not have bottle-brush chaetae and that it does have banana-shaped spines in the abdominal region.

Habitat: Central equatorial Pacific, 0°N 140°W, 4300m to 5°N 140°W, 4400m. Present predominantly in the 0-1 cm sediment layer.

Sp. 815

1 individual examined (BC#15 5°N 0-1cm EP106)

Description: Thoracic body shape swollen in anterior region. Prostomium deformed, shape not observed. Palps or scars not visible.

Thoracic notochaetae simple capillaries of 1-3 chaetigers in length, from chaetigers 6/7 long bottle-brush capillary chaetae greater than 8 chaetigers in length. Thoracic neurochaetae simple capillaries of about 1-2 chaetigers in length. Abdominal chaetae include acicular spines and banana shaped spines, do not form cinctures.

Remarks: Differs from the other species in this group in terms of the presence and position of the bottle-brush chaetae, differs from sp. 828 and sp. 827 in terms of the presence of banana-shaped spines.

Habitat: Central equatorial Pacific, 5°N 140°W, 4400m. Present in 0-1 cm sediment layer.

4.2.7 Group C – 'short simple capillary group'

Diagnosis: Short simple capillaries throughout, bottle-brush capillaries are absent

Sp. 811

3 individuals examined (BC#10 2°N 1-5cm EP046; BC#6 0°N 1-5cm EP050; BC#8 0°N 1-5cm EP098)

Description: Thoracic body region swollen in anterior region (chaetigers 1-6). Prostomium pointed, conical, tapering from peristomium. Buccal region 'tapers' gradually to form the prostomial point. Buccal region elongate. Palps sited less than two branchial widths from first chaetiger. Palp scars distinctive, large, longer than wide. Long thin branchiae arise in anterior thoracic region.

Thoracic notochaetae and neurochaetae simple capillaries of 1-2 chaetigers in length.

Remarks: Simplified species lacking morphological adaptations, long bottle-brush chaetae absent.

Habitat: Central equatorial Pacific, 0°N 140°W 4300m to 2°N 140°W 4400m. Present only in 1-5cm sediment layer.

Sp. 816

3 individuals examined (BC#11 2°N 1-5cm EP008; BC#16 5°N 5-10cm EP030; BC#12 2°N 1-5cm EP038)

Description: Thoracic body region slightly swollen in mid-region (chaetigers 5-10). Prostomium pointed, snout-like. Buccal region elongate, with thin mid-section. Palps less than two branchial widths from first chaetiger. Branchial scars visible on all thoracic chaetigers, sited 1 branchial width dorsal to notopodia.

Thoracic notochaetae and neurochaetae simple capillaries of 3-4 chaetigers in length.

Remarks: This species differs from sp. 811 in terms of the thoracic body shape and the shape of the prostomium.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m to 5°N 140°W, 4400m. Present within the 1-5 and 5-10 cm sediment layers.

4.2.8 Group D – 'bottle-brush chaetae group'

Diagnosis: Thoracic bottle-brush chaetae present; starting position of first bottle-brush chaetae variable.

Sp. 818

1 individual examined (BC#9 2°N 0-1cm EP018)

Description: Thoracic body shape with swollen anterior end, 'bullet' shaped appearance. Prostomium pointed, conical, tapering from peristomium. Buccal region compact. Palps more than two branchial widths from chaetiger 1. Branchial scars present to chaetiger 12.

Thoracic noto- and neurochaetae short capillaries of 1-2 chaetigers in length, from chaetiger 3 longer bottle-brush capillary chaetae greater than 10 chaetigers in length present.

Habitat: Central equatorial Pacific, 2°N 140°W 4400m. Present in 0-1cm sediment layer.

Sp. 829

3 individuals examined (BC#6 0°N 0-1cm EP067; BC#16 5°N 0-1cm EP012; BC#16 5°N 0-1cm EP016)

Description: Thoracic body shape swollen in posterior region. Prostomium pointed, snout-like. Buccal region elongate. Palps less than two branchial widths to chaetiger 1.

Thoracic notochaetae simple capillaries 3-6 chaetigers in length, from chaetiger 5 long bottle-brush chaetae greater than 10 chaetigers in length appear. Thoracic neurochaetae capillaries of length 4-5 chaetigers.

Remarks: Differs from sp. 818 in the thoracic body shape, the prostomium shape, the buccal region and the position of the palps.

Habitat: Central equatorial Pacific, 0°N 140°W, 4300m and 5°N 140°W, 4400m. Present in surface sediment layer only (0-1cm).

Sp. 831

3 individuals examined (BC#15 5°N 1-5cm EP084; BC#11 2°N 0-1cm EP93; BC#8 0°N 1-5cm EP 097)

Description: Thoracic body shape of uniform width throughout. Prostomium rounded. Buccal region elongate. Palps more than two branchial widths from first chaetiger. Branchial scars evident along entire body length, sited close to notopodia.

Thoracic notochaetae short simple capillaries 1-2 chaetigers in length, longer bottle-brush capillaries of 5-6 chaetigers in length from chaetiger 2. Thoracic neurochaetae simple capillaries of 1-2 chaetigers in length, also some slightly longer capillaries of 3-4 chaetigers in length.

Remarks: This species differs from sp. 818 and sp. 829 in terms of the thoracic body shape, the shape of the prostomium and the starting position of the bottle-brush chaetae.

Habitat: Central equatorial Pacific, 0°N 140°W, 4300m to 5°N 140°W, 4400m. Present in 0-1 and 1-5 cm sediment layers.

Sp. 823

7 individuals examined (BC#10 2°N 1-5cm EP042; BC#9 2°N 1-5cm EP036; BC#12 2°N 1-5cm EP037; BC#15 5°N 1-5cm EP087; BC#15 5°N 1-5cm EP081; BC#15 5°N 1-5cm EP079; BC#15 5°N 1-5cm EP080)

Description: Thoracic body shape hour-glass shaped. Prostomium shape conical. Buccal region elongate. Palps less than one branchial width from first chaetiger.

Thoracic notochaetae simple capillaries of 3-4 chaetigers in length, longer bottle-brush capillary chaetae from chaetiger 1. Thoracic neurochaetae 3-4 chaetigers in length.

Remarks: Limited range of characters available for this species. Differs from sp. 818, 829 and 831 in terms of the distinctive thoracic body shape, conical prostomium and the starting position of the bottle-brush chaetae.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m to 5°N 140°W 4400m. Present in 1-5 cm sediment layer only.

Sp. 817

2 individuals examined (BC#12 2°N 0-1cm EP028; BC#9 2°N 0-1cm EP017)

Description: Thoracic body shape uniform cylinder throughout. Prostomium pointed, conical. Buccal region elongate. Palps more than 2 branchial widths from first chaetiger. Thin branchial filaments arising from thoracic region.

Thoracic notochaetae simple capillaries of 1 chaetiger in length, also longer simple capillaries of 2-3 chaetigers in length, from chaetiger 9 longer bottle-brush capillary chaetae greater than 6 chaetigers in length appear.

Remarks: Species differs from sp. 818, 829 and 831 in terms of the thoracic body shape, the shape of the prostomium and the starting position of the bottle-brush chaetae. Differs from sp. 823 also in terms of the position of the palps.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m. Present only in 0-1 cm sediment layer.

Sp. 820

8 individuals examined (BC#6 0°N 0-1cm EP070; BC#15 5°N 1-5cm EP082; BC#6 0°N 0-1cm EP068; BC#20 9°N 0-1cm EP034; BC#6 0°N 0-1cm EP074; BC#19 9°N 0-1cm EP049)

Description: Thoracic body shape with swollen anterior end. Prostomium pointed, conical, tapering from peristomium. Buccal region elongate. Palps sited less than two branchial widths from first chaetiger.

Thoracic notochaetae simple capillaries 1-2 chaetigers in length, also simple capillaries of 2-3 chaetigers in length, from chaetiger 4 long bottle-brush capillaries greater than 6 chaetigers in length appear. Thoracic neurochaetae simple capillaries 1-2 chaetigers in length.

Remarks: Differs from sp. 829, 831, 823 and 817 in terms of the thoracic body shape, the prostomium shape and the starting position of the bottle-brush chaetae. Differs from sp. 818 in terms of the elongation of the buccal region and the position of the palps.

4.2.9 Group E – 'abdominal knob-tipped spine group'

Diagnosis: This group is characterised by the presence of abdominal knob-tipped spines. In concordance with Blake (1991) this places them in the genus *Tharyx.*

Sp. 832

1 individual examined (BC#11 2°N 0-1cm EP091)

Description: Thoracic body shape uniform width throughout. Prostomium pointed, conical. Buccal region compact. Palps not observed. Thin branchial filaments arise from thoracic region.

Thoracic noto- and neurochaetae simple capillaries 1-2 chaetigers in length. Abdominal noto- and neurochaetae thickened knob-tipped spines from chaetiger 14, also simple capillaries of 1-2 chaetigers in length.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m. Present in 0-1 cm sediment layer.

Sp. 836

1 individual examined (BC#9 2°N 0-1cm EP025)

Description: Thoracic body shape slightly swollen in posterior region. Prostomium pointed, conical. Buccal region elongate. Palps sited more than two branchial widths from first chaetiger.

Thoracic noto- and neurochaetae simple capillaries 1-2 chaetigers in length, from chaetiger 2 longer bottle-brush capillary chaetae greater than 5 chaetigers in length appear. Abdominal region moniliform, with chaetae forming cinctures of acicular spines, knob-tipped spines and simple capillaries of 1-2 chaetigers in length, cinctures in symmetrical arrangement with notopodial region of 2 or 3 capillaries for each acicular spine and neuropodia with 3 knob-tipped spines.

Remarks: This species differs from sp. 832 owing to the thoracic body shape, the elongation of the buccal region, the absence of bottle-brush chaetae and the presence of cinctures in the abdominal region.

Habitat: Central equatorial Pacific, 2°N 140°W, 4400m. Present in 0-1 cm sediment layer.

Sp. 819

7 individuals examined (BC#19 9°N 0-1cm EP048; BC#16 5°N 0-1cm EP013; BC#16 5°N 0-1cm EP015; BC#6 0°N 0-1cm EP071; BC#8 0°N 1-5cm EP102; BC#6 0°N 0-1cm EP066; BC#15 5°N 0-1cm EP105)

Description: Thoracic body shape swollen mid region (chaetigers 4-8). Prostomium pointed, snout-like. Buccal region elongate. Palps less than two branchial widths from first chaetiger.

Thoracic notochaetae simple capillaries of 1-3 chaetigers in length, from chaetiger 4 longer bottle-brush capillary chaetae greater than 5 chaetigers in length appear. Thoracic neurochaetae simple capillaries of length 2-3 chaetigers. Abdominal notochaetae include knob-tipped spines and simple capillaries of length 1-2 chaetigers, neurochaetae with banana-shaped spines, also simple capillaries of length 1-2 chaetigers.

Remarks: This species differs from sp. 832 and 836 in terms of the shape of the prostomium, the starting position of the bottle-brush chaetae and the presence of banana-shaped spines in the abdominal region.

Habitat: Central equatorial Pacific, 0°N 140°W 4300m to 9°N 140°W 4900m. Present predominantly in 0-1cm sediment layer.

4.2.10 Discussion

This case-study of deep-sea taxonomy has shown how it is possible to identify a difficult group to a putative species level using morphological characters. The major problem that was encountered was the lack of abdominal segments, in addition, better size ranges may be required to tease out potential allometric effects.

Hartman's (1961) definitions of the bi-tentaculate cirratulid genera *Tharyx, Chaetozone* and *Caulleriella* and Blake's (1991) revision (including the erection of a new genus, *Aphelochaeta*) are still under review. Unfortunately, it was not possible to accurately identify the genus for the EqPac specimens as a result of the absence of certain characters, in particular the arrangement of the abdominal spines. In addition, there remains some confusion over the generic diagnoses for *Chaetozone*; Malmgren, 1867, included no generic description (Woodham and Chambers, 1994). A redescription of *Chaetozone setosa* (the species for which the genus was erected) is currently underway (Chambers, pers. comm.). Until such generic revisions have been completed, there is little point in attempting to define genera for the EqPac species, simple groupings have been indicated for practical purposes only.

The diversity of this cirratulid group is remarkably high, considering the limited range of habitats and food resources available in the deep-sea ooze. 18 species were recorded from the 17 EqPac box-core samples and 22 species were recorded from the 24 north-east Atlantic box-cores. Fauchald and Jumars (1979) predicted that

> *"...all cirratulids will be found to be surface deposit-feeders using their palps for food collecting. We also expect that they will show selectivity, both in terms of particle composition and in the size of the particles."*

For the EqPac samples at least, there was little or no evidence to suggest that particle selectivity was taking place. Where gut contents were observable, they appeared of a uniform variety showing no species specific variation. However, there was some evidence that different species may be inhabiting different layers of the sediment. Sp. 810, 824, 812, 823, 816 and 814 where found within the sediment (1-5 cm and 5-10 cm layers). Sp. 829, 828, 827, 815, 817, 818, 836, 832 and 819 were found within the 0-1 cm surface layer and top water. Only sp. 814, 831 and 820 where found inhabiting both layers.

This result suggests that there may be some vertical profiling of the niche spaces of these deep-sea cirratulids, indicating at possible mechanisms of diversity maintenance; this is discussed further in chapter 6. It seems probable that these deep-sea animals are both burrowing and surface deposit feeders.

Within the Cirratulidae, a variety of reproductive modes are used. *Dodecaceria*, for example, may reproduce asexually through fragmentation and regeneration or sexually as an epitoke (Gibson and Clark, 1976). The majority of species of cirratulid are gonochoristic. In externally fertilising species, development may take place within the sediment, as in *Tharyx marioni* or pelagically as in *Cirriformia tentaculata* (Blake, 1975). Larvae are generally thought to be non-feeding, whether benthic or planktonic.

The range of information from shallow-water studies of reproduction indicate the difficulties in using such studies as analogues for deep-water systems. There have been no studies of reproduction in abyssal cirratulids. At the EqPac sites there is likely to be both seasonal and interannual variations in food input to the benthos, hence there is a potential for selection pressures for seasonal reproduction. No evidence of reproductive processes was observed in the specimens, however, more individuals of the same species would be required to properly answer these questions and to look for potential cohorts in size classes. In addition, the lack of time-series data limits the potential for reproductive studies, an important aspect of community structure in the deep sea.

4.3 A New Species of *Sigambra* (Polychaeta: Pilargidae) from North Atlantic Abyssal Plains

4.3.1 Introduction

In this section, a traditional Linnean taxonomic approach has been adopted for an abundant species from the north-east Atlantic. It was conspicuous in being one of the more abundant species and certainly the dominant predator. The species was widespread being recorded from study sites from the Cape Verde Abyssal Plain at 20°N to the Porcupine Abyssal Plain at 48°N.

4.3.2 Methods and material studied.

The collection methods are as described in section 3.1.2. The holotype specimen was from the Porcupine Abyssal Plain, 4844 m at 48° 51.5' N 16° 29.6' W discovered in the 1-3 cm layer. Paratypes were examined from the Porcupine Abyssal Plain, the Tagus Abyssal Plain (38°N 11°W, 5035 m), the Madeira Abyssal Plain (31° 10' N 21° 10' W, 4985 m) and the Cape Verde Abyssal Plain (20° N 30° W, 4500 m). A total of 51 individuals were examined.

In addition, the following material was examined: *Sigambra bidentata* Britaev & Saphronova, 1981 (Sea of Japan), *Sigambra gracilis* Britaev & Saphronova, 1981 (Vostok Bay, Sea of Japan) and *Sigambra phuketensis* Licher and Westheide, 1997 (Phuket Island, Thailand).

4.3.3 Taxonomic account

Family: PILARGIDAE

Genus: *Sigambra* Müller, 1858

Species: *S. magnuncus* sp. nov.

4.3.4 Description

Holotype length 3.7 mm for 33 chaetigers, paratypes ranged from 0.5 mm for 13 chaetigers to 10.5 mm for 50 chaetigers.

Body unpigmented, slightly flattened anteriorly, but becoming more rounded posteriorly; anterior chaetigers widest.

Prostomium rounded, slightly indented laterally at junction of palps and prostomium. Palps biarticulate with relatively long palpostyles; palpophores fused distally over half their length. Three antennae, median antenna longest, situated slightly posterior to laterals in smaller specimens, but more level with them in larger individuals. A pair of cushion like nuchal organs, situated on either side of the median antennae. Eyes absent. Pharynx without jaws, armed with eight equal size, slightly pointed papillae.

Peristomium approximately twice as long as first chaetiger. Two pairs of long tapering tentacular cirri, dorsal cirri longer than ventral, and slightly shorter than median antennae. A row of low cushion-like papillae (sense organs) extend across dorsal surface of peristomium (may only be visible under high magnification).

Parapodia biramous; anterior parapodia laterally orientated, becoming more dorsal in median and posterior chaetigers. A row of cushion-like papillae extending across dorsal surface between notopodia on each chaetiger.

Notopodia pointed, with straight, blunt-tipped internal aciculae. Dorsal cirri of chaetiger 1 long, thin and tapering; nearly equal in length to median antennae; subsequent dorsal cirri initially shorter with wider bases, but in posterior chaetigers becoming more slender and longer. Large hooks emergent on chaetiger 3 (Figures 4.3, 4.4). In posterior chaetigers, hooks meet in midline. Short, delicate capillaries projecting from most notopodia, just one in anterior chaetigers, usually becoming two in posterior segments.

Neuropodial lobes pointed with blunt-tipped, straight internal aciculae (Figures 4.5). Ventral cirri absent on chaetiger 2; on other chaetigers ventral cirri thin and tapering, equal to or shorter than neuropodia, equal to or slightly longer than dorsal cirri. Neurochaetae simple capillaries slightly expanded at the base, tips of chaetae quickly taper into a prolonged point (Figure 4.5)

Pygidium with two tapering cirri. Anus dorsal.

Distribution: S. *magnuncus* has been recorded from the abyssal plains of the north east Atlantic at depths from 4000 m to 5085 m.

Etymology: The name derives from the large conspicuous hooks on the notopodia (Latin *magnus* – large, *uncus* – hook).

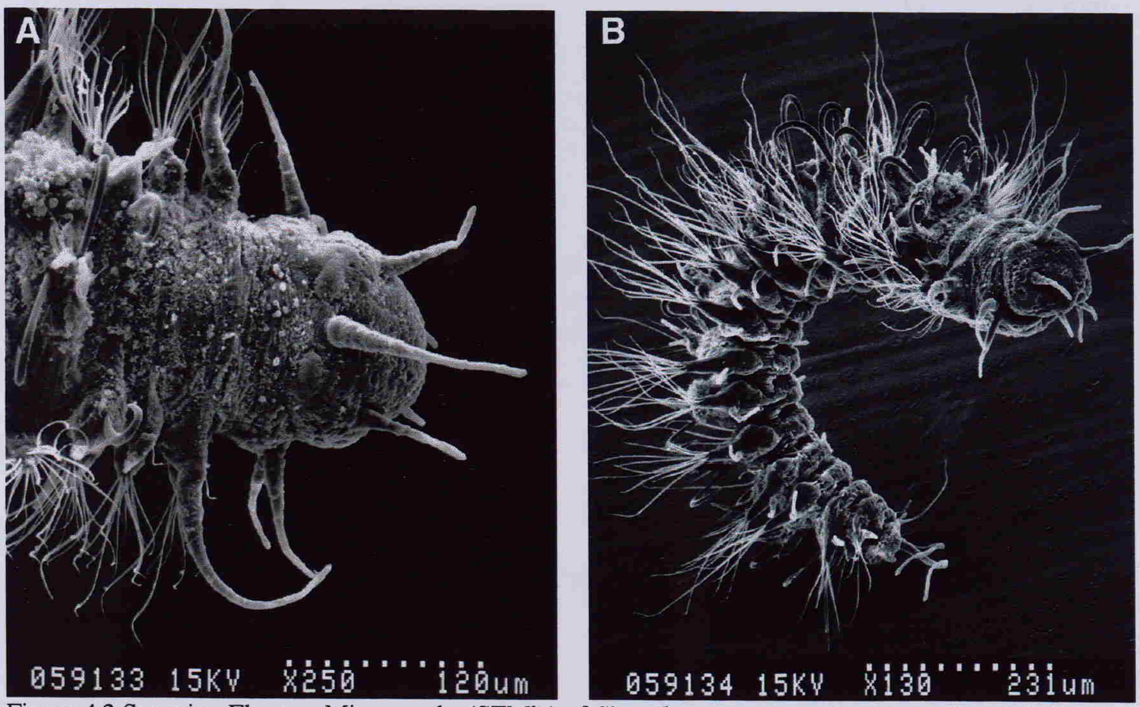


Figure 4.3 Scanning Electron Micrographs (SEM's) of *Sigambra magnuncus* (specimen from MAP site). A, dorsal view of anterior region. B, general view of individual.

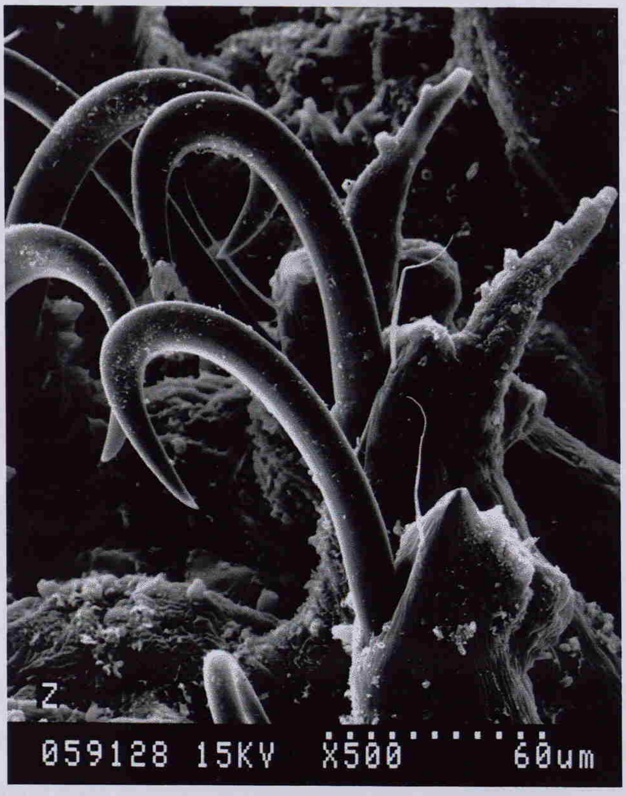


Figure 4.4 SEM of *Sigambra magnuncus* showing view of notopodia. Note small capillary chaetae in each notopodium.

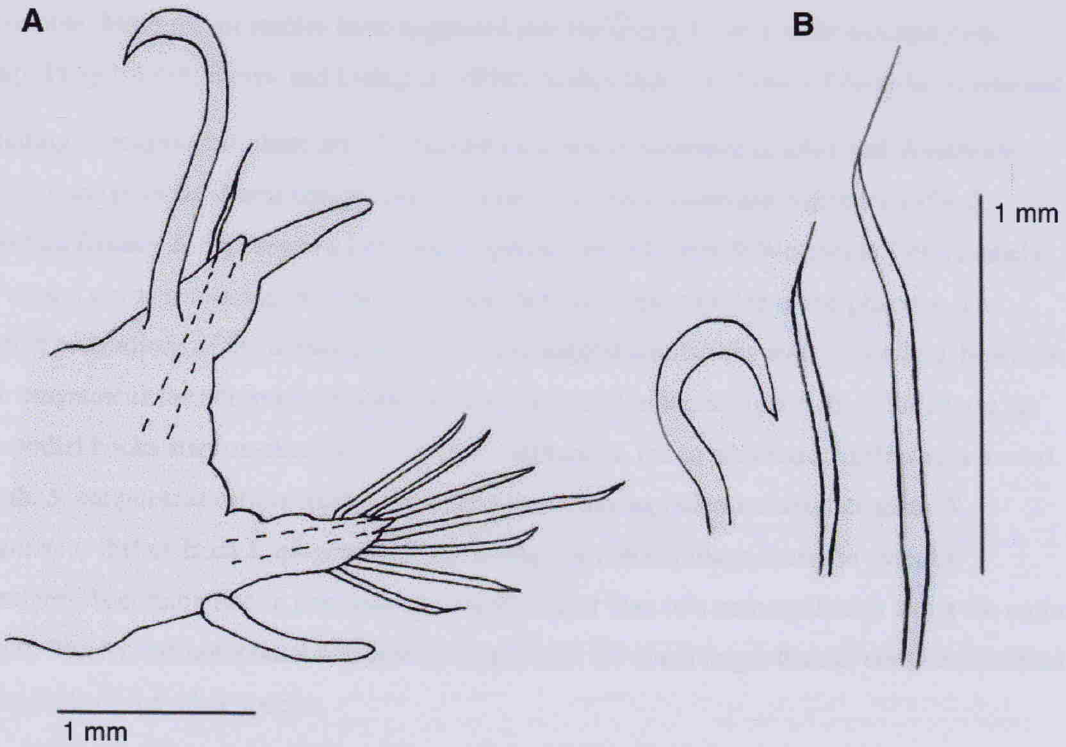


Figure 4.5 A, parapodium from mid region, anterior view. Bar = 0.1 mm. B, chaetae – notopodial hook and neurocapillaries.

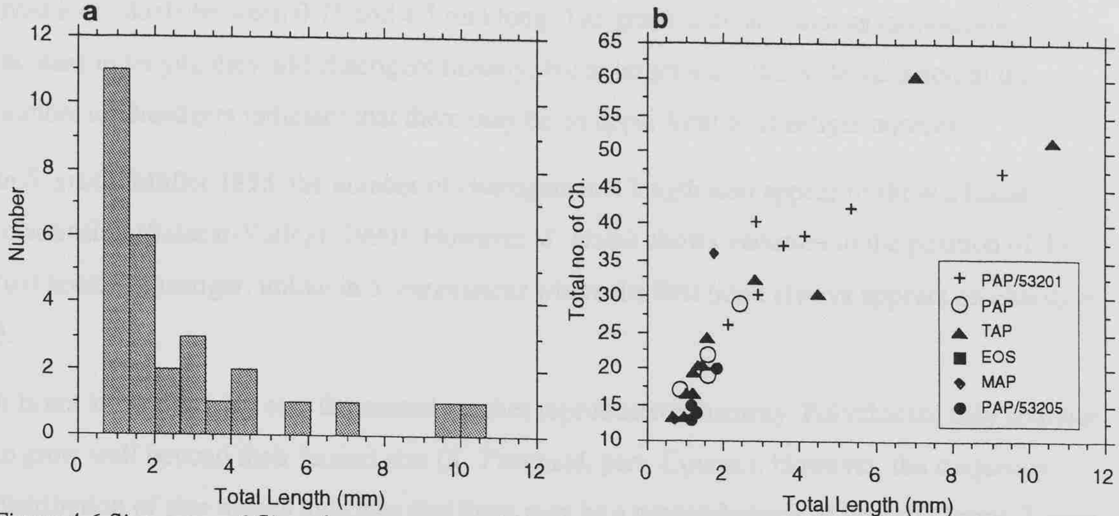


Figure 4.6 Size range of *Sigambra magnuncus*: (a) size frequency distribution of total animal length, (b) allometric growth plot indicating the relationship between the number of chaetigers and total length.

4.3.5 Discussion

It has been suggested that the family Pilargidae is paraphyletic unless included in the family Hesionidae (Licher and Westheide, 1994). However, this hypothesis was based on a study where the outgroup taxon used to root the cladogram was also a hesionid. It is not possibly to test for the paraphyly of pilargids with respect to hesionids unless the hesionid taxa are also included in the ingroup. Rooting the trees using the hesionids makes any such analysis impossible. More recent studies have suggested that the pilargids are a valid monophyletic group (Pleijel, 1998; Pleijel and Dahlgren, 1998). In this study, the family Pilargidae is retained.

Including *S. magnuncus*, there are 17 described species of *Sigambra* (Licher and Westheide, 1998). *S. magnuncus* shares certain features with *S. ocellata* Hartmann-Schröder 1959, *S. bidentata* Britaev & Saphronova 1981 and *S. qingdaoensis* Licher & Westheide 1997, namely the ventral cirrus is missing on chaetiger 2 and there are eight papillae in the pharynx. The relative proportions of the dorsal and ventral cirri suggest similarities with *S. ocellata*, however, in *S. magnuncus* the notopodial hooks start on chaetiger 3, not chaetiger 6. In *S. bidentata* the notopodial hooks start on chaetiger 3, as in *S. magnuncus*, but in addition to differences in cirri length, *S. magnuncus* differs from *S. bidentata* in not having bidentate neurochaetae. *S. magnuncus* differs from *S. qingdaoensis* in having one notocapillary chaeta in anterior chaetigers, becoming two in posterior chaetigers, rather than two notocapillaries along the entire length. Finally, the notopodial hooks in *S. magnuncus* are much larger than in comparable sized individuals of the other species.

S. magnuncus was most common in box core samples from the Porcupine and Tagus abyssal plains with densities ranging from 4 to 32 individuals per m^2. At the more southerly sites, it was much rarer, partly as a result of the lower overall polychaete densities at these sites. The animal was most commonly found within the sediment rather than on the sediment surface. Allometric changes are shown in Figure 4.7. The size of the specimens ranged from 0.5 to 10.5 mm, with most individuals between 0.75 and 4.5 mm long. The graph indicates that as individuals increase in length, they add chaetigers linearly, but at larger sizes the wide variation in the number of chaetigers indicates that there may be an upper limit to chaetiger number.

In *S. grubii* Müller 1858, the number of chaetigers and length also appear to show a linear relationship (Salazar-Vallejo, 1990). However, *S. grubii* shows variation in the position of the first hooked chaetiger, unlike in *S. magnuncus* where the first hook always appears on chaetiger 3.

It is not known at what size the animal reaches reproductive maturity. Polychaetes may continue to grow well beyond their fecund size (K. Fauchald, pers. Comm.). However, the frequency distribution of size ranges indicates that there may be a preponderance of juvenile forms. Larger specimens may be too sparsely distributed to be collected in any numbers by the small box core samples, making analysis of size cohorts difficult. Nevertheless, this is one of the few species collected in numbers high enough for an analysis of growth to be undertaken. There is evidence to support the hypothesis that the great majority of individuals collected by the box core are, even if not strictly speaking juveniles, several orders of magnitude smaller than their potential largest size. This hypothesis is explored further in Chapter 5.

4.4 General Discussion

The purpose of this chapter was to highlight the approach used and the limitations of the morphological taxonomic method. The following chapters on the diversity and community structure of deep-sea polychaete assemblages must be evaluated in the light of these limitations. It is apparent that putative morphological species may be identified. However, morphologically identical species may in fact be different, as in the sibling species of *Capitella capitata* (Grassle and Grassle, 1977), although in many cases subsequent more detailed analyses of morphology have resolved these issues.

Many of the controversies and discussion surrounding diversity rest on the species concept, taxonomy and classification. A more rigorous theoretical framework is probably required before the total biodiversity question can be properly addressed. Better preserved specimens with better size ranges is necessary, as is molecular analysis.

Deep-sea specimens appear to lack the range of characters often found in shallow-water forms (Hartman, 1965; Hartman and Fauchald, 1971). To understand biogeographic patterns, new approaches are probably required. Either, there is less emphasis on the quantitative aspect of deep-sea sampling – i.e. collections are geared towards gathering specimens for taxonomy rather than abundance – or molecular approaches are utilised, as in Etter *et al.* (1999). Diversity itself may be better tested at molecular levels. The question centers on the aspect of biodiversity that is actually of interest. In this study, the morphological diversity of clades of individuals (putative species) has been measured. Whilst there is no doubt that this is an important aspect of diversity, it is certainly not the only one. In the future, it may be possible to show that diversity at the genetic level is even higher, with many morphologically identical sibling species in the deep sea. Alternatively, many of the putative morphological species may in fact be phenotypes of the same species. In addition, better knowledge of feeding ecology may indicate that diversity at a functional level is quite low; if many of the polychaetes in the system are living in the same space and eating the same food then there is probably considerable 'redundancy' in the community.

A large research effort is required to understand these other aspects of diversity. Examining morphology and erecting putative species hypotheses, as done here, is a necessary first step. But to fully understand the processes structuring deep-sea communities a better understanding of the animals that live there is required. Most of the questions regarding deep-sea ecology revolve around understanding the type and scale of animal interactions. These interactions can only be studied once a reasonable taxonomic understanding has been established. It is not known, for example, how *Sigambra magnuncus* reproduces or what it feeds on. It may be an important predatory species with a significant functional role within the community, or it may be an opportunistic scavenger. A few calculations serve to illustrate why it might be an important species. *S. magnuncus* is known to be widespread across abyssal sites in the north-east Atlantic. The Atlantic has an area of approximately 80,000,000 km^2. Assuming that the north-east Atlantic region represents one-quarter of this total area then this equates to a habitat for *S. magnuncus* of approximately 20,000,000 km^2, or 2×10^{13} m^2. Estimating the density of *S. magnuncus* to be at the lower end of the range, i.e. 10 individuals per m^2, then there are 2×10^{14}, or 200 trillion individuals in the north-east Atlantic. Using mean values for the length and width of the worm, and treating it as a cylinder, the volume of an individual equates to about 0.3 mm^3. Hence the total volume of all the *S. magnuncus* in the north-east Atlantic is about 6×10^{13} mm^3 or 60,000,000 litres, which is approximately 60,000 metric tonnes (wet weight) of the animal. Although there are undoubtedly inaccuracies in these calculations, they are, if anything an underestimate, as the species may have a much larger range than just the north-east Atlantic. Species that are both abundant and widespread will contribute significantly to the total biomass of the deep sea, and their potential functional role cannot be ignored.

5 DENSITY, GROWTH AND SIZE OF ABYSSAL POLYCHAETES

5.1 Introduction

The central Pacific and north Atlantic regions exhibit marked spatial and temporal variability in surface water productivity (Figures 5.1 and 5.2). The central hypothesis of this chapter is that this productivity is the key controlling variable affecting polychaete density and body size on the seabed 4 km below.

Rutgers University's Ocean Primary Productivity group have used the formula of Behrenfeld and Falkowski (1997) to convert SeaWIFS chlorophyll measurements into measures of surface primary production[7]. These data, combined with the estimates of sea-surface temperature (SST) anomalies for the equatorial Pacific estimated by the Climate Prediction Centre at the United Kingdom Meteorological Office[8] are shown in Figure 5.1. Surface primary production is strongly correlated with the SST anomalies during 1997-1999. 1997/1998 is the most comparable year to the 1992 EqPac sampling program (when no data are available from the SeaWIFS), in that the first half of the year is a warm SST El Niño and the second half a cool SST La Niña. In 1999, cool La Niña conditions dominated throughout the year. As of July 2000, La Niña conditions still prevail in the central Pacific, an unprecedented length of time for La Niña. The EqPac stations 0°N, 2°N and 5°N are most likely to be influenced by this temporal variability in production. At 9°N, HOT 23°N, DOMES A, ECHO 1, and PRA there is little temporal variability in surface production, although there was inexplicably enhanced production during March-May 1999 over the 9°N and DOMES A sites.

In the north Atlantic (Figure 5.2), the most pronounced temporal change is a seasonal one with a large phytoplankton bloom occurring in the north-east Atlantic during March-May and continuing until September. There is little, or at least undocumented, interannual variation, although the bloom off the west coast of Africa is larger in 1999 than in 1998.

Although it is the spatial variation that is being measured in this study, interannual variations in surface productivity mean that simple annual averages of productivity are not suitable for comparative purposes. For example, an annual average production level for 1997/98 at EqPac 0°N would be much lower than that for 1998/99. In the following sections, measurements of year round averages are compared with those from the three months preceding the sampling period as predictors of benthic processes. At all sites, the 1997/98 year has been used as it is most closely related to the conditions that were prevalent during the 1992 El Niño. 1997/98 does not appear to be particularly unusual with regard to the north Atlantic sites.

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[7] http://marine.rutgers.edu/opp/

[8] http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.html

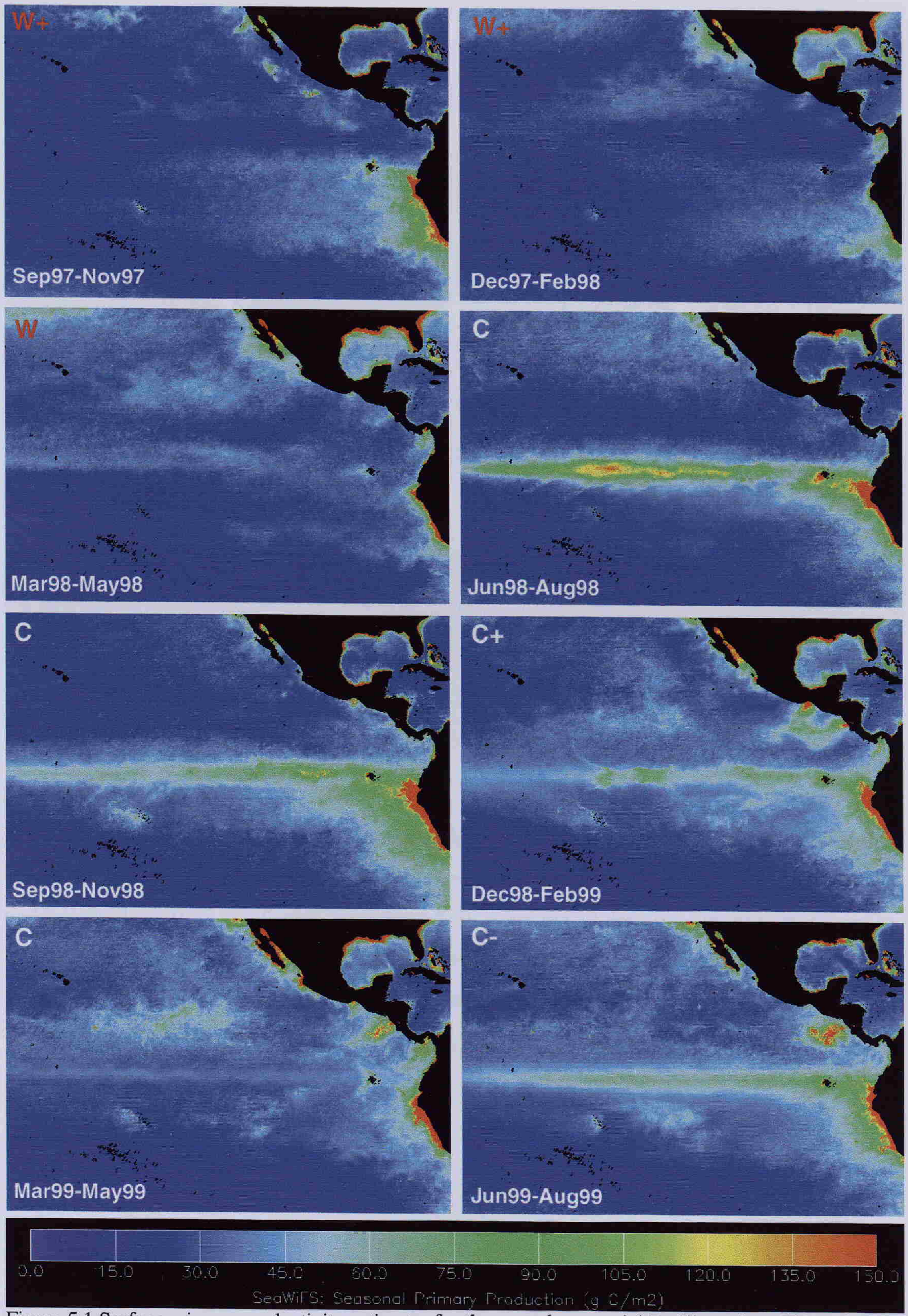


Figure 5.1 Surface primary productivity estimates for the central equatorial Pacific region. (W) and (C) refer to warm (El Niño) and cool (La Niña) SST anomalies, + and - refer to the strength of these anomalies. Data on productivity from Rutgers University - Ocean Primary Production group; SST data from the UK Meteorological Office.

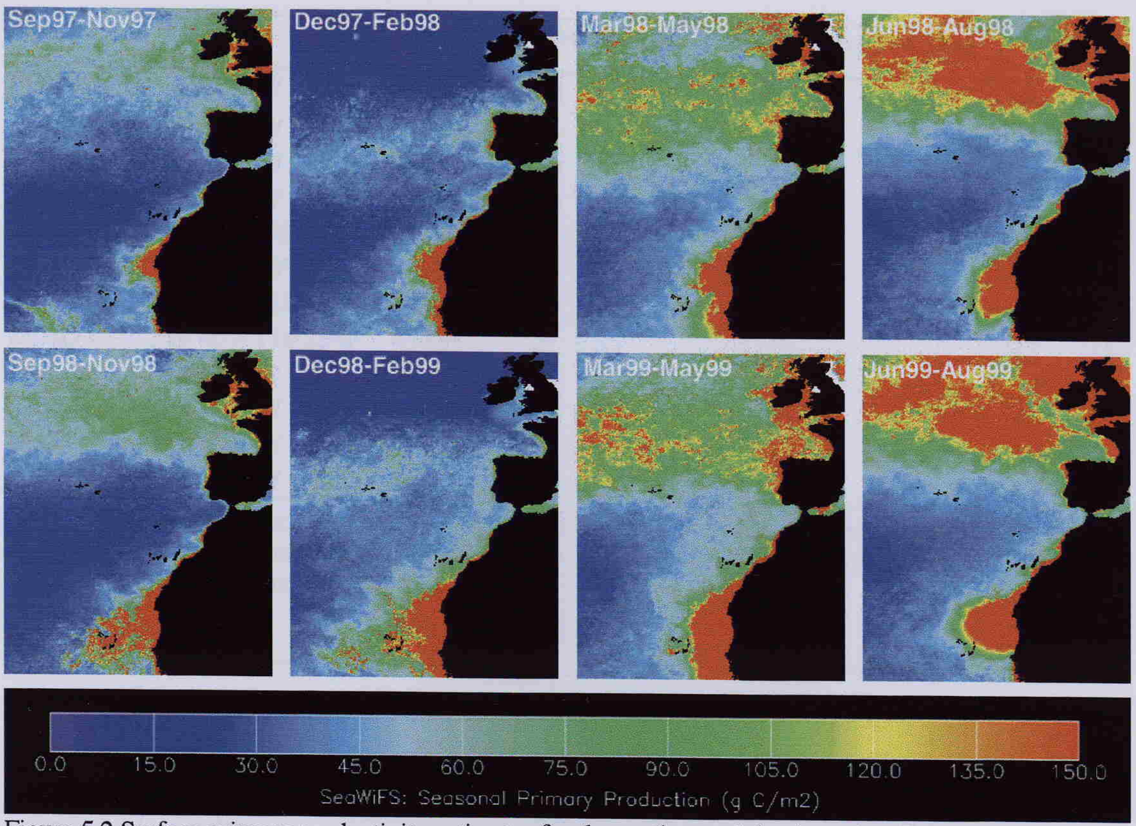


Figure 5.2 Surface primary productivity estimates for the north-east Atlantic region. Data on productivity from Rutgers University - Ocean Primary Production group.

5.2 Results

5.2.1 Density

The highest densities were recorded from the PAP and EqPac 0°N sites (85 and 83 individuals 0.25 m^{-2} respectively). The lowest densities were from the EqPac 9°N and HOT 23°N sites (13 and 9 individuals 0.25 m^{-2}) (Table 5.1, Figure 5.3). Note that all densities are those measured by counting the number of individuals that were identified to species level. These values were used as many of the original datasets excluded any unidentifiable specimens. The proportion of species identified varied from 62-70% at EqPac, and the real values for EqPac only are indicated in Table 5.1.

Site	Position	Depth	*Abundance 0.25m^{-2}	Abundance 0.25 m^{-2}	S.D	n
EQPAC 0°N	0°N 140°W	4300m	136	83	48	3
EQPAC 2°N	2°N 140°W	4400m	86	59	13	4
EQPAC 5°N	5°N 140°W	4400m	112	79	19	3
EQPAC 9°N	9°N 140°W	4900m	17	13	4	3
HOT 23°N	23°N 158°W	4800m	13	9	3	4
DOMES A	8°27'N 150°47'W	~5000m		16	6	47
PRA	12°57'N 128°19'W	4800m		65	22	15
ECHO 1	14°40'N 126°25'W	4500m		42	17	15
PAP	48°N 16°W	4800m		85	20	5
TAP	38°N 11°W	5035m		65	26	8
MAP	31°N 21°W	4900m		17	8	5
EOS	20°N 30°W	4600m		36	10	6

Table 5.1 Density of polychaetes per box core (0.25 m^{-2}). * indicates those measurements of total number of individuals including unidentifiable specimens. Note that the values for the EqPac, HOT and TAP were corrected to allow for the reduced sampling area.

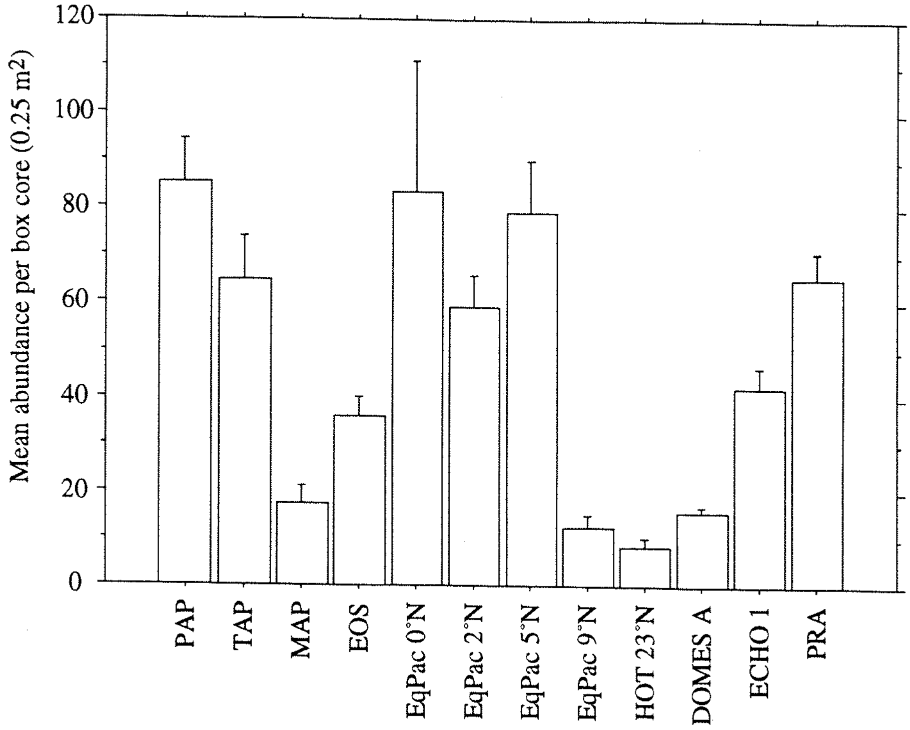


Figure 5.3 Density of polychaetes per box core (0.25 m^{-2}). Error bars are ±1S.E.

Increasing surface production led to an increase in benthic polychaete densities at both Atlantic and Pacific sites (Figure 5.4). However, there is a considerable degree of scatter, and the data indicate that surface production and density may be more strongly coupled in the Pacific than Atlantic oceans, although there are not enough data points in the Atlantic for this to be confirmed. There is an improvement in the R^2 value for the Pacific data when productivity is measured using estimates for the three months prior to sampling. The PAP site has the highest productivity estimates in terms of annual averaged values and for the three month period prior to sampling, although the density is no higher than at the less productive EqPac sites. Excluding PAP, the three month production estimates appear to be a better predictor of polychaete density than annual average estimates.

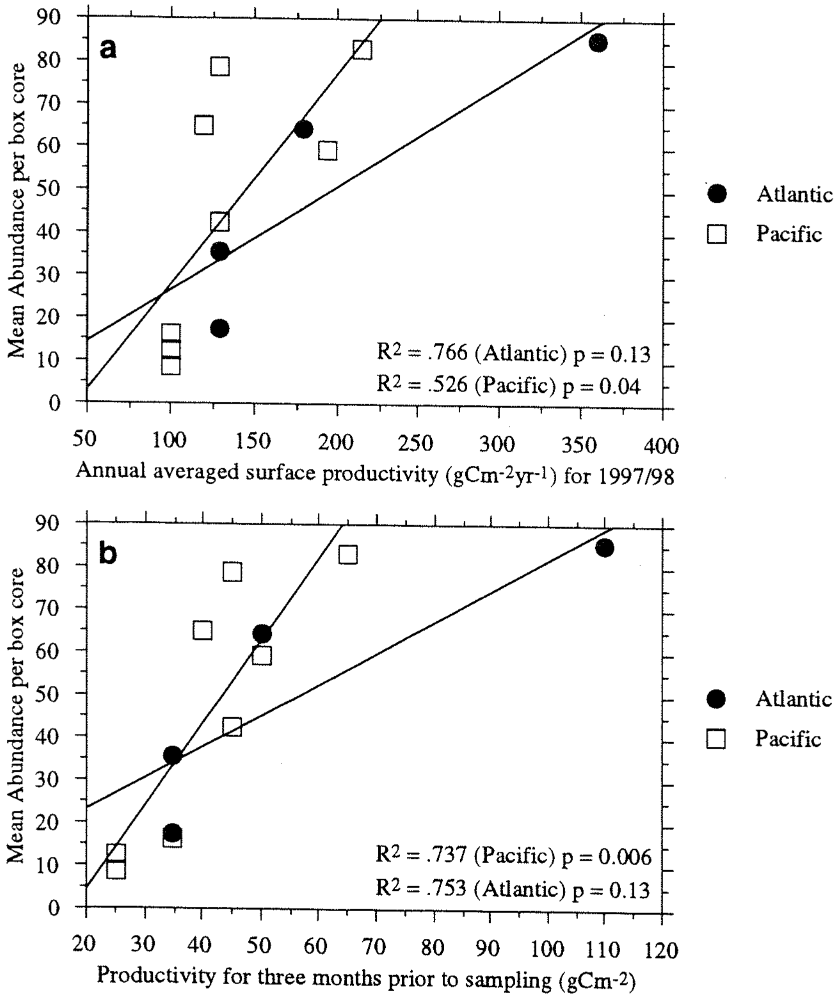


Figure 5.4 The relationship between benthic polychaete density and (a) annual averaged surface production and (b) production estimated for the three months prior to sampling. Separate regression lines plotted for Atlantic and Pacific sites. The relationship is only significant at $p<0.05$ for Pacific sites.

Excluding the north Atlantic PAP site from the analysis leads to a much closer relationship between surface production and polychaete density (Figure 5.5). In addition, there is a close relationship between averaged annual POC flux and polychaete density. However, there is only a limited dataset available for POC flux and it has been suggested that measurements taken using different methods are not comparable (Lampitt, pers. comm.). For the EqPac sites, where POC flux data are comparable and were measured over an entire year (Honjo *et al.*, 1995), there is a close relationship between POC flux and polychaete density.

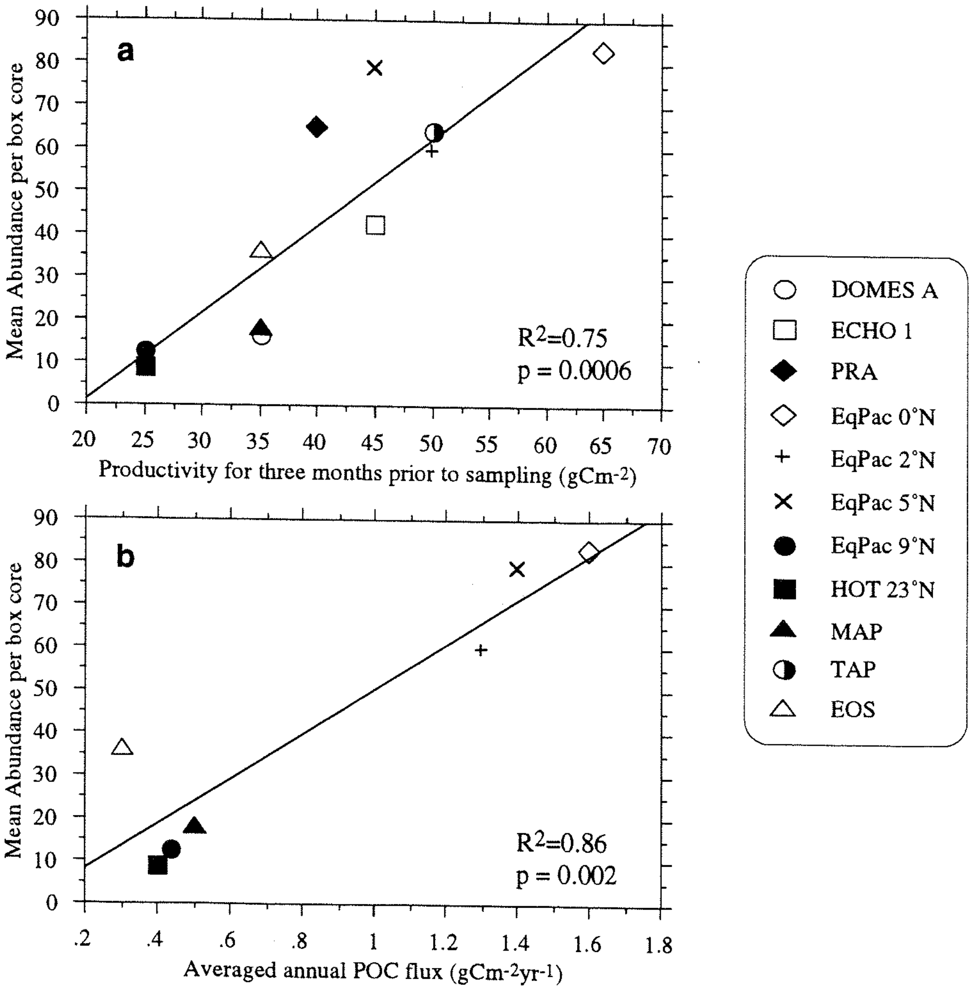


Figure 5.5 Relationship between (a) surface production and polychaete density and (b) averaged annual POC flux and polychaete density. Note that PAP site has been excluded from these analyses.

The relationship between surface production and POC flux (Figure 5.6) reinforces the suggestion that benthic-pelagic coupling is tighter in the Pacific ocean than in the Atlantic ocean. A doubling of surface production in the Pacific ocean leads to an increase in POC flux of 3 1/2 times. In then north Atlantic, a three-fold increase in production leads to only a 2 1/2 times increase in POC flux.

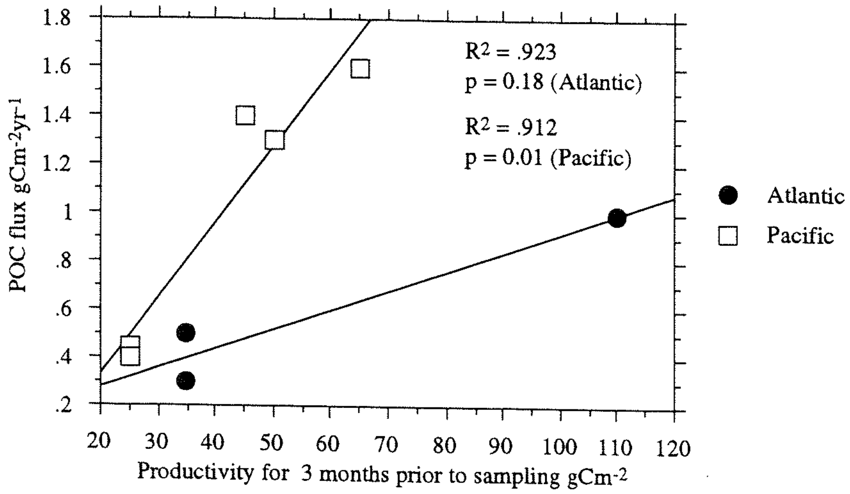


Figure 5.6 Relationship between surface production and average annual POC flux in the Atlantic and Pacific oceans (separate regression lines).

5.2.2 Growth and body size at EqPac

The great majority of specimens were fragmented, hence it was not possible in many cases to measure the entire length of the worm. For this reason, a suitable proxy for total body size was investigated. The width of the first chaetiger was the best predictor of total body length in those specimens that were whole (Figure 5.7). The first chaetiger width was also a good predictor of the volume of the first ten chaetigers, and conformed to the allometric power transformation model (log-log) (Figure 5.7). This indicates that there is initially a linear relationship between width and volume, but at larger volumes, chaetiger width is more important than length. The worms initially increase length, and then later increase width, as was seen for *Sigambra magnuncus* (Chapter 4).

At EqPac, 842 individuals were measured by the author. Of these, all but 6 had a first chaetiger width between 0.06 – 1 mm. These remaining six (*Scoloplos* sp. 843; *Sphaerodorum* sp. 878; Capitellid sp. 882; *Glycera* sp. 952) were several orders of magnitude larger, between 6 - 17 mm in width and comparable in size to shallow-water species. Smaller specimens of these large species were not found. The implications of this discontinuity in size distributions are explored further in section 5.3. For the purposes of the remaining analyses, these specimens were excluded as they were outliers to the main distribution, representing only 0.7% of the fauna, but with a mean first chaetiger width over ten times larger than the remaining 99.3%.

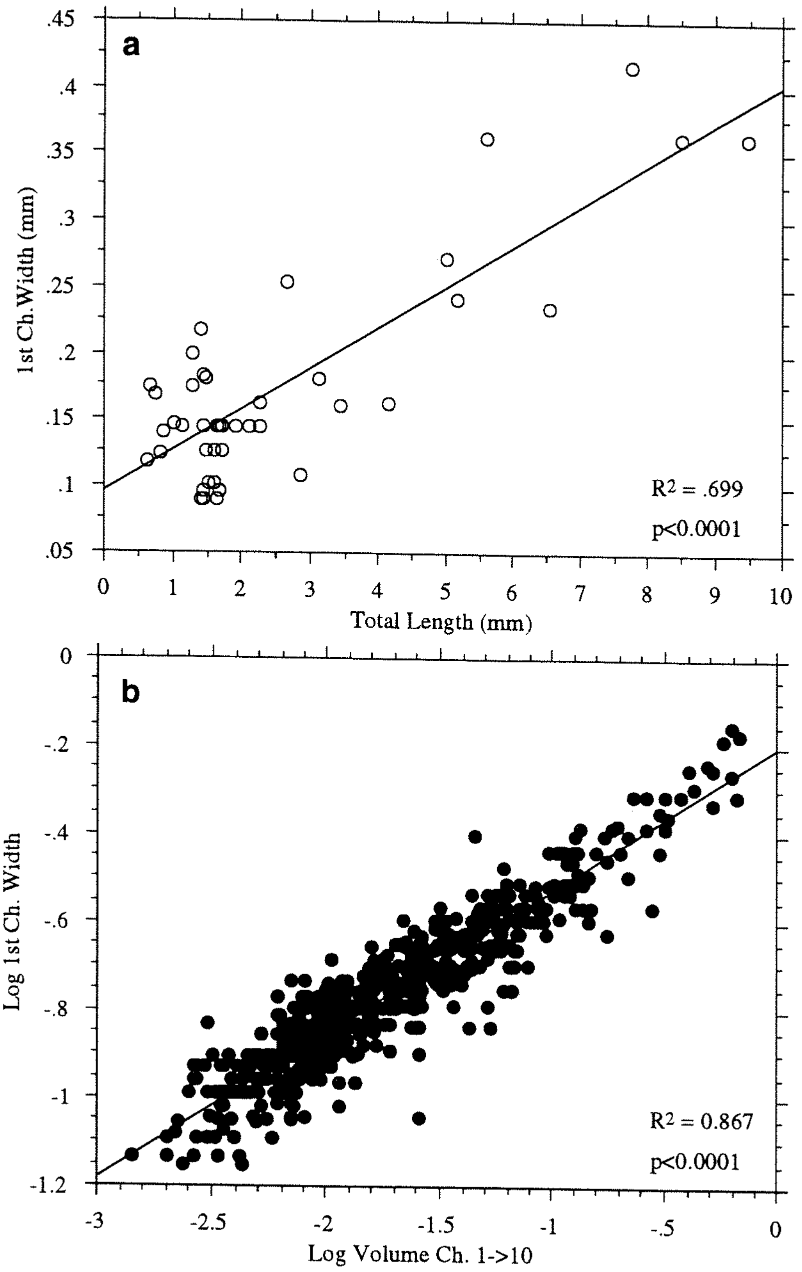
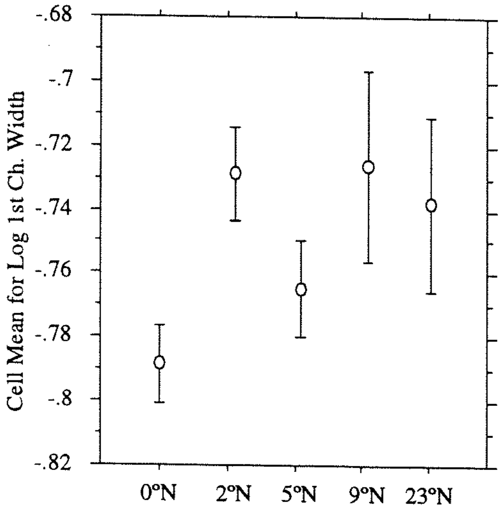


Figure 5.7 The relationship between (a) 1st chaetiger width and total body length (linear regression) and (b) 1st chaetiger width and volume of first ten chaetigers (power transformation). The greater number of datapoints in the second graph is a reflection of the many more individuals that could be measured for the first ten chaetigers only (fragmented worms).

Log transformations of 1st chaetiger width and volume have been used to normalise the data. All size data conformed to the log-normal model. Polychaetes were significantly larger at 2°N versus 0°N, but no other significant differences between sites were found (ANOVA $p>0.05$, Figure 5.8). When the phytodetrital sites 0°N, 2°N and 5°N are pooled and compared with the low productivity sites (9°N and 23°N) no significant difference is found (ANOVA $p>0.05$). The reduced size at 0°N is the result of an increased percentage of sabellid polychaetes at this site (Table 5.2) that contribute 11% of individuals at 0°N, and only 3-4% at 2°N and 5°N. Sabellids are the smallest polychaetes in the EqPac abyss, with a mean width of just 156 µm.



	Mean Diff.	Crit. Diff	P-Value	
0°N, 23°N	-.050	.086	.2514	
0°N, 2°N	-.060	.037	.0018	S
0°N, 5°N	-.024	.037	.2024	
0°N, 9°N	-.062	.077	.1152	
23°N, 2°N	-.009	.087	.8357	
23°N, 5°N	.026	.087	.5505	
23°N, 9°N	-.012	.110	.8365	
2°N, 5°N	.036	.039	.0719	
2°N, 9°N	-.002	.078	.9521	
5°N, 9°N	-.038	.078	.3384	

Figure 5.8 Plot of log mean width (mm) at EqPac sites, ANOVA-Fisher PLSD post-hoc test of significance. Error bars are ±1S.E. 'S' denotes significance at the $p<0.05$ level.

	Total %	**0°N %**	**2°N %**	**5°N %**	**9°N %**	**HOT 23°N %**
Spionidae	19	18	14	25	17	12
Cirratulidae	17	18	20	14	14	4
Paraonidae	13	12	15	13	10	19
Syllidae	13	11	11	13	13	30
Acrocirridae	7	6	8	6	3	15
Sabellidae	6	11	3	4	3	0
Others	25	24	29	25	40	20

Table 5.2 Percentage contributions of the top 6 dominant families at EqPac and HOT.

The relationship between food input and body size was explored further by splitting the analysis between families, and grouping the sites into those that receive phytodetritus and those that do not (Figure 5.9). For the Spionidae and Paraonidae, there was a significant reduction in body size at phytodetrital sites, there were no other significant differences, although there was a general trend for reduced size in syllids and sabellids at the phytodetrital sites. In real terms, there was a decrease in the mean width of the spionids and paraonids of 30 and 20 percent respectively in the phytodetrital sites.

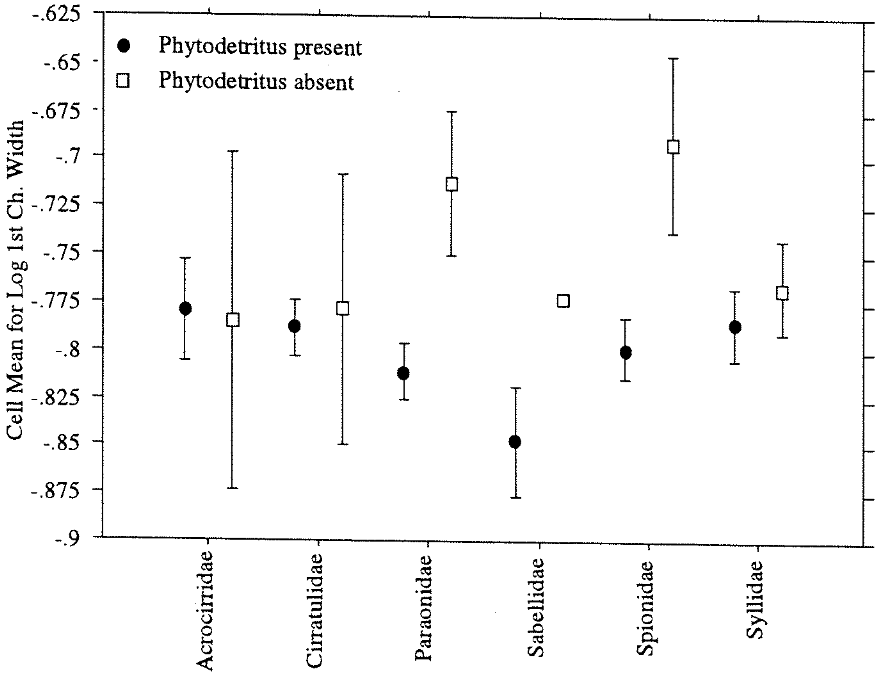
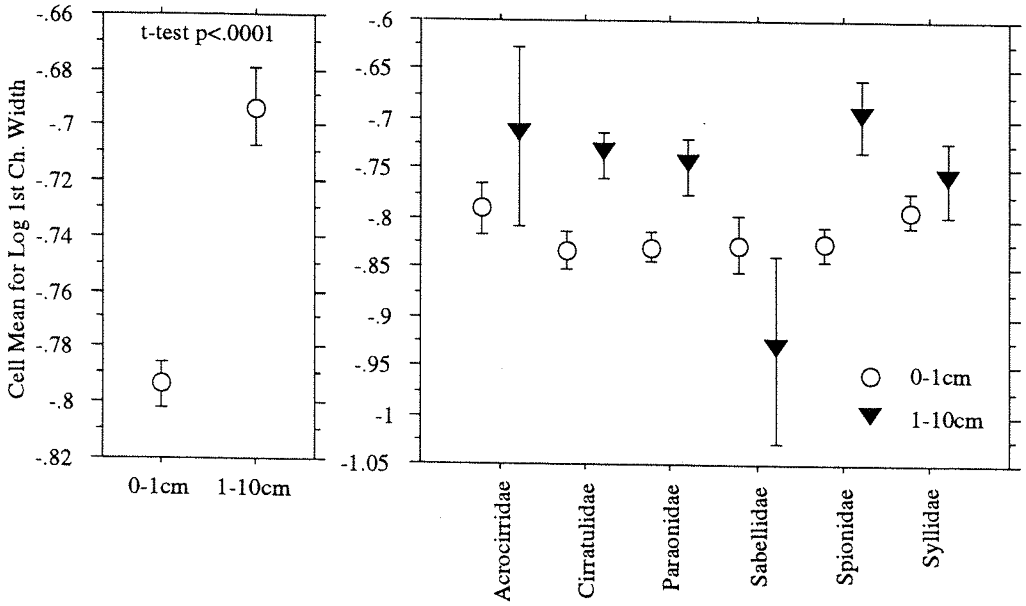


Figure 5.9 Mean body size at Phytodetrital and non-phytodetrital sites, split by family. For individual families, t-test p<0.05 for Spionidae and Paraonidae, other families show no significant differences. Error bars are ±1S.E.

Very few polychaetes were present in the 5-10cm layer and it was deemed suitable to pool these together with those in the 1-5cm layer to permit a comparison of surface dwellers with sediment dwellers. There was a significant increase in body size in the deeper layers of the sediment (Figure 5.10). In real terms, this translated to an increase of twenty percent in the deeper layers. This increase in size was significant (t-test p<0.002) for the Paraonidae, Cirratulidae and Spionidae (Figure 5.10). Other families showed a trend towards increasing size, but not statistically significant. There were very few Sabellids in the deeper sediment layers. For individual species, only the top 5 were selected (Figure 5.11). There was a trend towards increasing body size for all of these species, but only statistically significant for *Prionospio* sp. 886, which was abundant across sediment layers. In summary, it appears that sediment dwelling species are larger in size than surface dwellers, and that those species that are present in both layers also show an increase in size in the deeper layers.



	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Family	5	.293	.059	2.225	.0507	11.125	.725
Depth Layer (2)	1	.179	.179	6.807	.0094	6.807	.748
Family*Depth Layer (2)	5	.311	.062	2.363	.0390	11.813	.756
Residual	506	13.306	.026				

Figure 5.10 ANOVA interaction analysis for log body size with vertical profile and family. Cirratulidae, Paraonidae and Spionidae are all significantly larger in the 1-10cm layer. Error bars are ±1S.E.

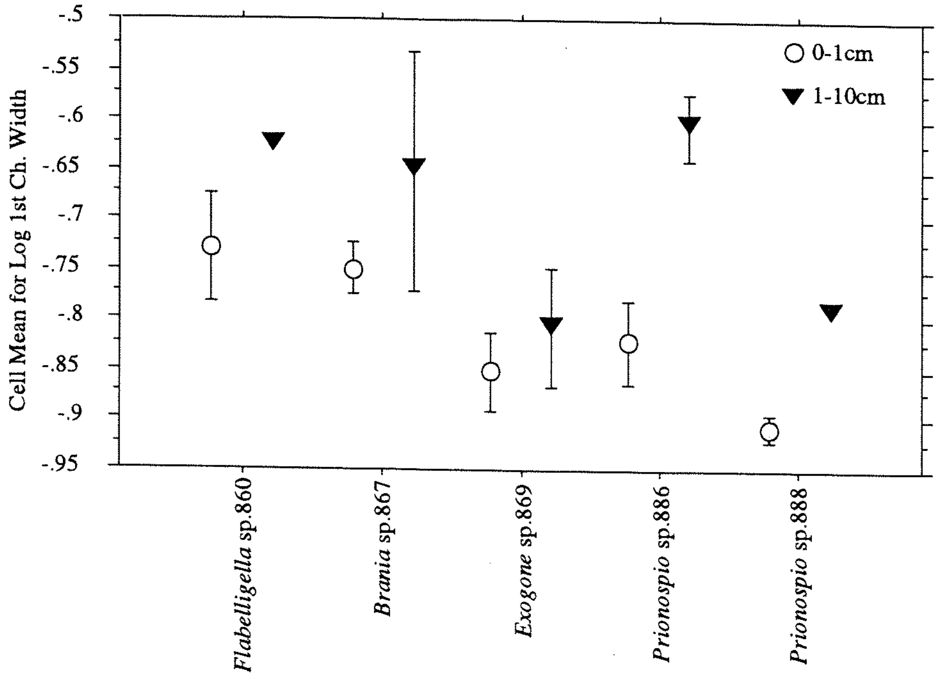
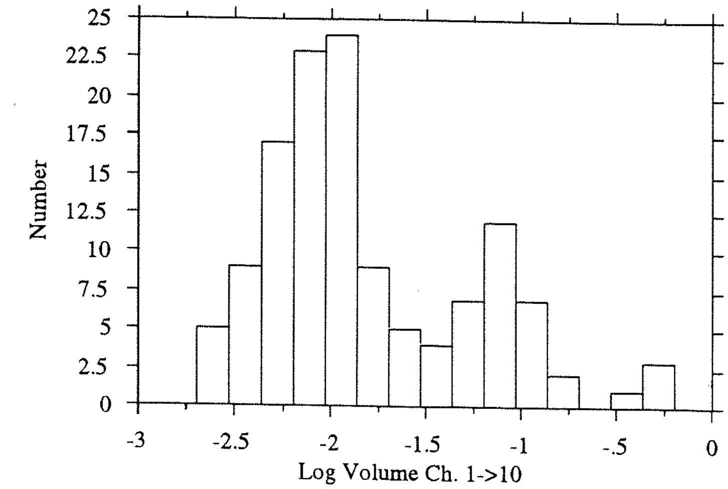
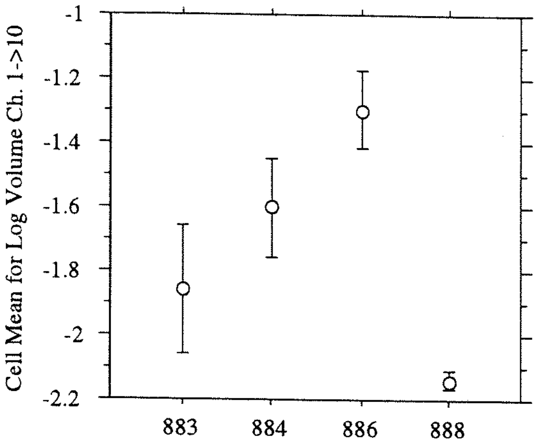


Figure 5.11 Log body size in the five most abundant species; only *Prionospio* sp. 886 is significantly larger in deeper depth layers. Error bars are ±1S.E.

The spionids were the only family to show a discontinuity in size distributions (Figure 5.12). Two peaks are visible, the smallest at a log volume of –2 to –2.2 (in real terms, 0.01 mm^3 to 0.006 mm^3) followed by a peak of larger individuals at –1 to –1.5 (0.1 mm^3 to 0.03 mm^3). Analysis of variance for the size of the four most abundant spionid species (all of the genera *Prionospio*) indicates that *Prionospio* sp. 888 has a smaller mean size than the other species. The next largest is sp. 883, followed by sp. 884 and the largest is sp. 886. The only non-significant difference is that between sp.883 and sp.884.



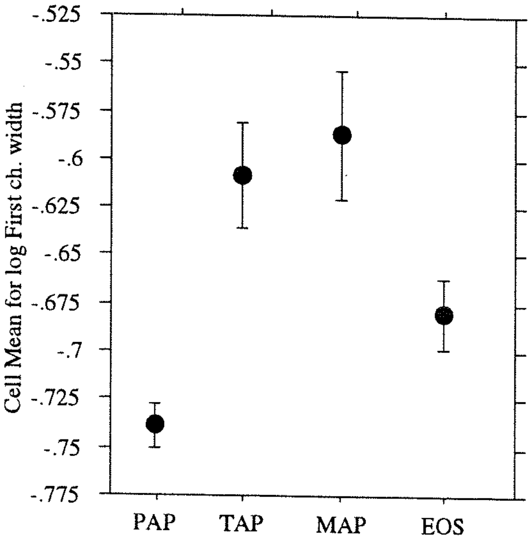


	Mean Diff.	Crit. Diff	P-Value	
883, 884	-.255	.321	.1172	
883, 886	-.558	.297	.0004	S
883, 888	.282	.256	.0312	S
884, 886	-.303	.286	.0381	S
884, 888	.537	.243	<.0001	S
886, 888	.840	.211	<.0001	S

Figure 5.12 Size distribution of Spionidae; ANOVA post-hoc Fisher PLSD test on log body size for dominant spionid species at EqPac. The small, but abundant sp. 888 results in the two-peaked distribution. Error bars are ±1S.E. 'S' denotes significance at the p<0.05 level.

5.2.3 Growth and body size in the north Atlantic

In the north Atlantic, body size was smallest at the PAP site and largest at the MAP site, which was not significantly different from the TAP site; polychaetes at EOS were intermediary in size between PAP and TAP/MAP (Figure 5.13). In real terms, polychaetes were 15% smaller at PAP than at EOS, and 28% smaller than at TAP and MAP.



	Mean Diff.	Crit. Diff	P-Value	
EOS, MAP	-.092	.068	.0082	S
EOS, PAP	.059	.044	.0085	S
EOS, TAP	-.071	.058	.0172	S
MAP, PAP	.151	.063	<.0001	S
MAP, TAP	.021	.074	.5715	
PAP, TAP	-.130	.052	<.0001	S

Figure 5.13 Mean body size (log of 1st chaetiger width) at north Atlantic sites; ANOVA Fisher PLSD post-hoc test of significance; all significant (denoted by 'S') at $p<0.05$ level except MAP and TAP. Error bars are ±1S.E.

Considerable variation in the abundance of different families exists in the north Atlantic. As at EqPac, cirratulids, spionids, paraonids and sabellids are amongst the dominant six families, generally accounting for 60-70% of the fauna (Table 5.3). Unlike EqPac (Table 5.2, previous section), syllids and acrocirrids are not especially abundant, and opheliids and pilargids are more common.

Sabellids are the most variable in size of the north Atlantic abyssal polychaetes; strongly influencing the observed between-site pattern (Figure 5.14). In real terms, the sabellids varied in size from a mean width of 79 μm at TAP to 250 μm at EOS. Cirratulids and spionids are also significantly smaller at PAP than at other sites, in real terms, 20% and 10% respectively.

	Total Percent	PAP Percent	TAP Percent	MAP Percent	EOS Percent
Cirratulidae	28	32	21	9	35
Spionidae	19	23	17	21	11
Paraonidae	11	10	12	16	10
Sabellidae	8	9	1	5	11
Opheliidae	4	2	11	0	3
Pilargidae	4	1	12	2	1
Others	27	23	26	48	28

Table 5.3 Percentage of total number of individuals for top 6 dominant families at north-east Atlantic abyssal sites.

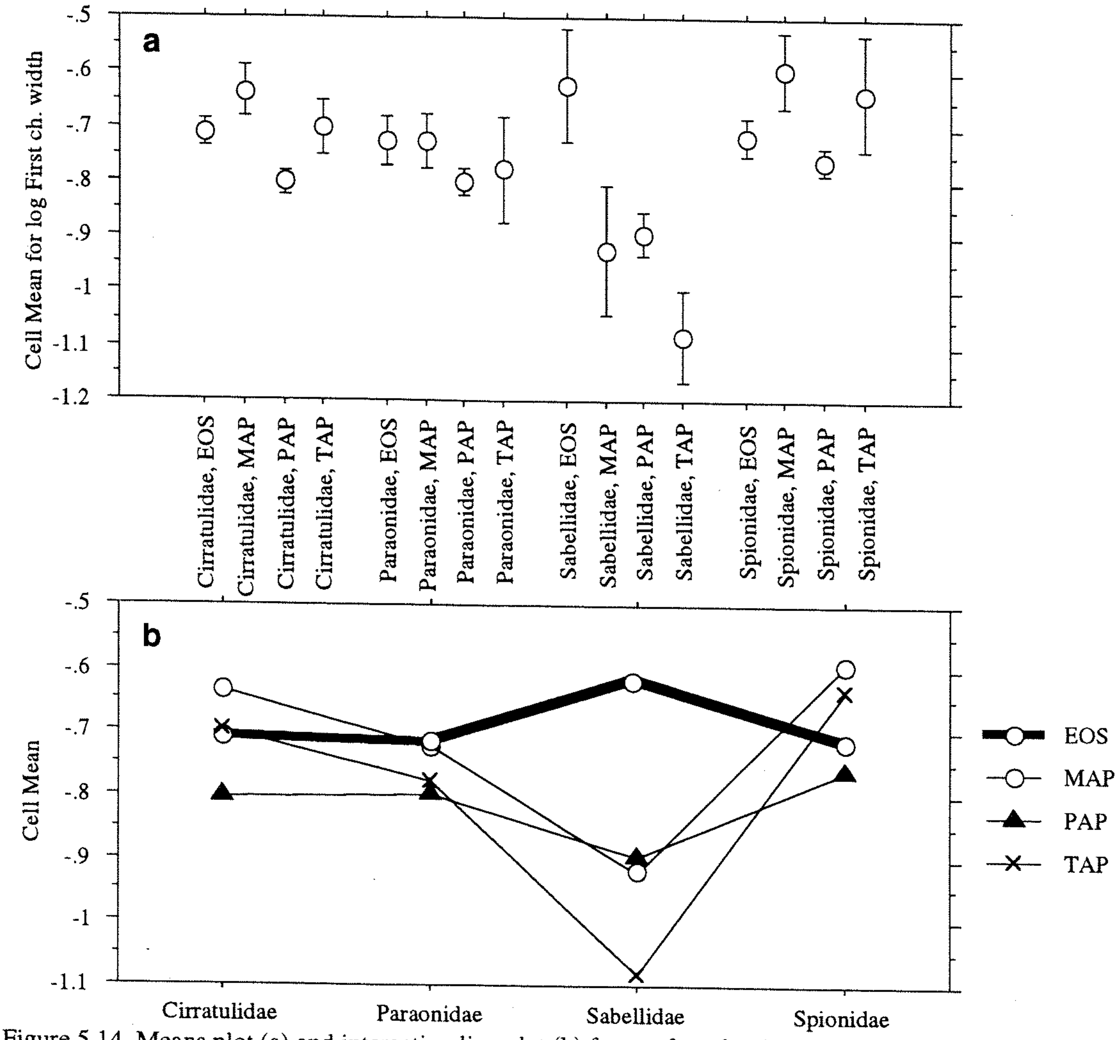


Figure 5.14 Means plot (a) and interaction line plot (b) for top four dominant families in the north-east Atlantic; Sabellids are the most variable sized polychaetes. Error bars are ±1S.E.

An analysis of body size variability in individual species is presented in Figure 5.15. Out of the eight most dominant species, six showed reduced body size in phytodetrital sites, while two showed increased body size in the phytodetrital sites. The two species that showed increased body size at phytodetrital sites are predatory species – a syllid and a pilargid polychaete. All the other species are surface deposit feeders. In real terms, the north Atlantic species *Chaetozone* sp.55 had a mean width of 200 μm at the non-phytodetrital sites and 155 μm at the phytodetrital sites. *Aricidea* sp. 601 had a mean width of 220 μm at the non-phytodetrital sites, and 112 μm at the phytodetrital sites. *Prionospio* sp. 613 had a mean width of 257 μm at the non-phytodetrital sites, and 165 μm at the phytodetrital sites. The abundant EqPac polychaete *Flabelligella* sp. 857 had a mean width of 240 μm at the non-phytodetrital sites, and 128 μm at the phytodetrital sites. The north Atlantic predatory polychaete *Sigambra* sp. 8 showed the opposite trend to these species: an *increase* in size from the non-phytodetrital sites (mean 200 μm) to the phytodetrital sites (281 μm).

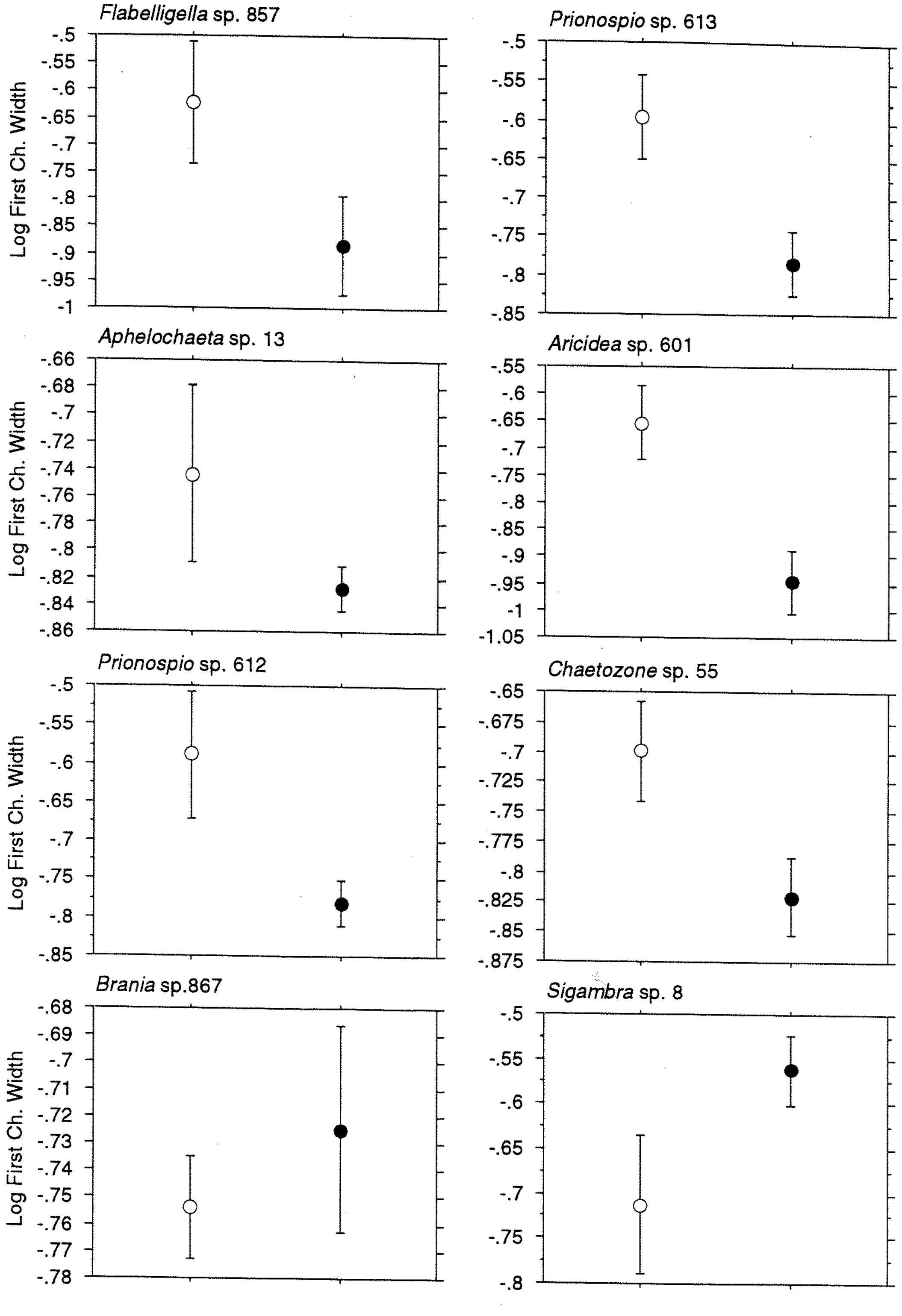
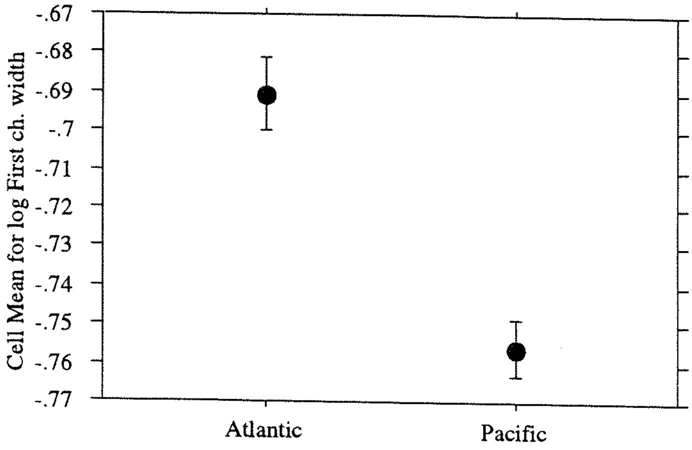


Figure 5.15 Body size variation for individual dominant species in the north Atlantic and EqPac sites. All dominant species show reduced body size in phytodetrital samples (black filled circles), except for sp. 867 and sp. 8 which show reduced body size in non-phytodetrital samples (open circles). Error bars are ±1S.E.

5.2.4 Comparison of body size between Pacific and Atlantic abyssal sites

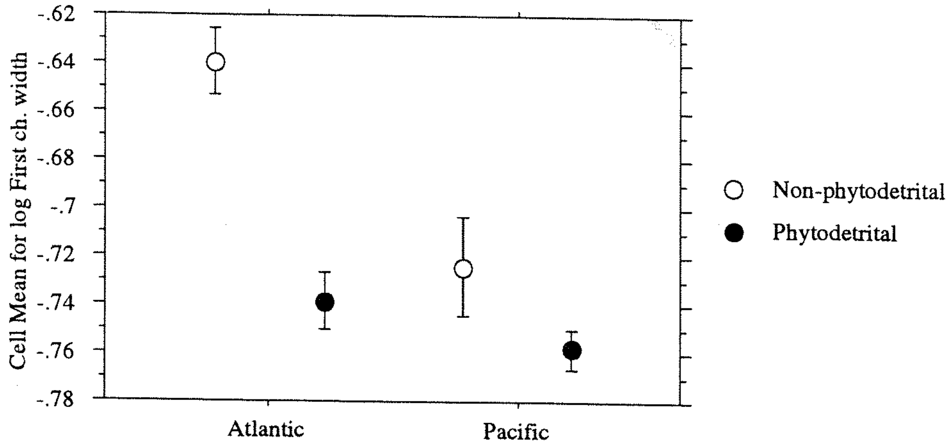
Polychaetes are 13% larger in the Atlantic than in the Pacific (Figure 5.16).



	Mean Diff.	DF	t-Value	P-Value
Atlantic, Pacific	.065	1341	5.460	<.0001

Figure 5.16 Mean polychaete body size in the Atlantic and Pacific oceans; t-test indicates significantly larger worms in the Atlantic than in the Pacific. Error bars are ±1S.E.

Phytodetrital input (which is also associated with high production) appears to strongly influence polychaete body size in the north Atlantic, and less strongly in the Pacific (Figure 5.17). Polychaetes are smaller in phytodetritus rich sites (PAP, EqPac phytodetrital sites). The overall difference in size between the Atlantic and Pacific oceans is caused primarily by the increased numbers of large polychaetes at the non-phytodetrital Atlantic sites.



	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Ocean	1	.390	.390	8.388	.0038	8.388	.841
Food Effect	1	.634	.634	13.642	.0002	13.642	.974
Ocean * Food Effect	1	.149	.149	3.207	.0735	3.207	.415
Residual	1339	62.253	.046				

Figure 5.17 Mean body size in Atlantic and Pacific oceans, split by type of food input (phytodetrital sites PAP and EqPac 0°N, 2°N, 5°N and non-phytodetrital sites – all others). ANOVA table indicating significant effect of both food and ocean basin. Error bars are ±1S.E.

5.3 Discussion

Sibuet *et al.* (1989), in a review of benthic data from the Atlantic ocean, concluded that

> *'The first order relationship between meiofaunal and macrofaunal abundance can be explained by a direct relationship with a common trophic input.'*

Brown *et al.* (in press) have shown how nematode abundance is 50% lower in the central Pacific gyre regions compared to the food-rich EqPac phytodetrital sites. With this in mind, it is no surprise that polychaetes show enhanced abundance at the food rich EqPac phytodetrital sites (Figure 5.3), and that density at EqPac site 0°N is amongst the highest yet discovered.

Polychaete density was found to vary from just 9 individuals per box core at EqPac 9°N to 85 individuals at the north Atlantic PAP site. In contrast to Brown *et al.*'s data on nematodes, polychaete density is over 90% lower at central Pacific gyre regions than at the EqPac phytodetrital sites, indicating a potentially much stronger relationship between polychaete density and organic carbon input and surface production. The large variability in polychaete densities across the abyss appears to best explained by this spatio-temporal variability in surface production.

The problem in establishing a close link between surface production and benthic abundance is that the 'missing link' data on POC flux is usually insufficient both spatially and temporally. Uniquely, at the EqPac site, Honjo *et al.* (1995) have provided POC flux measurements from sediment traps moored over an entire year across the entire transect. Variability in abundance at EqPac can be viewed as the benchmark with which to understand variability at the less well studied manganese nodule and north Atlantic areas.

5.3.1 Surface production and benthic abundance as proxies for POC flux

The scarcity of adequate data on POC flux (Lampitt and Antia, 1997) indicates that this may be the most difficult of the three variables to measure. The USNEL spade box core is a remarkably simple and reliable device allowing accurate and comparable measurements of benthic abundance to be made. Few would argue that the box core is the only sampling gear that should be used, and as will be shown in a later section, it may well be missing a significant portion of the larger motile polychaetes. But for comparative purposes, it is arguably the state of the art. Similarly, the advent of satellite based ocean colour sensors, coupled with formulas for the conversion of colour measurements to ground-truthed estimates of production (Behrenfeld and Falkowski, 1997) allows ocean productivity to be measured anywhere on the planet, over temporal scales of months to years.

Unfortunately for the EqPac study, there were no satellites flying during the 1992 cruise programme. Nevertheless, measurements of sea surface temperature made through the NOAA's network of moored buoys, coupled with direct measurements of temperature and production made on ship have indicated that the 1992 year was dominated by El Niño conditions for the first six months, followed by a weakened El Niño and enhanced surface production during the latter half of the year (Barber *et al.*, 1994). This pattern corresponds closely to the conditions prevalent in 1997/98, during the first year of operation for the SeaWIFS satellite. For the north Atlantic and manganese nodule sites, there is little inter-annual variation in production, hence there is no reason to suggest that 1997/98 should not be used as a proxy for these sites also.

Using the production values for three months prior to the sampling programme and performing a regression analysis against polychaete abundance (Figure 5.4) indicates that productivity explains about 75% of the variance in the Pacific, and 73% in the Atlantic. The comparison between using annual average productivity and productivity for three months prior to sampling indicates that for the Pacific data, annual average production is less useful as a predictor of abundance, explaining only 53% of the variance. The likely explanation for this patterns is that the benthic fauna is responding primarily to variations in the strength of the phytoplankton bloom, and hence is less well correlated with yearly averaged figures, which are strongly influenced by the length of the El Niño period. This is potentially indicative of the 'response time' of polychaetes to a bloom event, which may be on a scale of months. Certainly the phytodetrital material reaches the seabed very quickly, on a scale of days, as has been shown by Rice *et al.* (1986) and Smith *et al.* (1996). This concept is explored further in the final section of this chapter.

The north Atlantic site PAP appeared to be an outlier to the main distribution. Productivity at PAP is nearly twice as high as at EqPac 0°N, yet abundance is virtually identical. Excluding the PAP site from the analysis leads to a close relationship between productivity and abundance for all the abyssal sites treated together (Figure 5.5).

This observation is best explained using the data on POC flux (Figure 5.6). Benthic-pelagic coupling appears to be much tighter in the Pacific than in the Atlantic. PAP has unusually low levels of POC flux considering the extremely high productivity values observed during the spring bloom. Lampitt and Antia (1997) suggested that at very high levels of productivity, above 200 $gCm^{-2}yr^{-1}$, productivity ceases to have an effect on POC flux at 2000m depth (Figure 5.19). They put forward three reasons why this might be so – (1) increasing dependence on regenerated nutrients at high levels of productivity, (2) increased degradation rate of particles between the surface and 2000m, possibly caused by increased consumption by mesopelagic animals and (3) enhanced horizontal advection of material in areas of high productivity. The data on benthic polychaete abundance from PAP supports the observations of Lampitt and Antia (1997).

The relationship between abundance and surface productivity has been further explored using additional already published data from the Pacific and Atlantic (Table 5.4; Figure 5.18, below).

When the oceans are treated individually, it can be seen that in the Pacific Ocean the best fit regression line is steeper than that for the Atlantic sites. A doubling of surface productivity in the Pacific leads to a quadrupling of benthic abundance; in contrast, doubling of Atlantic surface production leads only to a 1.8 times increase in abundance.

SITE	**Polychaetes 0.25m^{-2}**	**Productivity gCm^{-2} for 3 months prior to sampling**	**Reference**
Atlantic			
PAP	86	110	This study, Paterson *et al.* (1998)
BIS 4200	102	110	Laubier and Sibuet (1979)
TAP	65	50	This study, Paterson *et al.* (1998)
MAP	18	35	This study, Glover et. al (in press)
EOS	36	35	This study, Paterson *et al.* (1998)
DEM A	41	35	Sibuet *et al.* (1984)
DEM B	21	35	Sibuet *et al.* (1984)
VEN-Turb.	33	30	Richardson and Young (1987)
VEN-Pel.	36	30	Richardson and Young (1987)
Pacific			
EqPac 0°N	83	65	This study
EqPac 2°N	59	50	This study
EqPac 5°N	79	45	This study
EqPac 9°N	13	25	This study
HOT 23°N	9	25	This study
CLIMAX II	16	25	Hessler and Jumars (1974)
DOMES	23	35	Hecker and Paul (1979)
DOMES A	16	35	Wilson and Hessler (1987)
ECHO 1	43	45	Wilson and Hessler (1987)
PRA	66	40	Wilson (1990)

Table 5.4 Abyssal polychaete abundance, data from this study and other published sources. Only sites between 5000m and 3500m have been used, all were samples taken with USNEL spade box core.

This hypothesis is further explored in the final graph in Figure 5.18. Rather than there being a different relationship between the oceans, it is apparent that when all the sites are treated together, a linear relationship holds until productivity values reach a threshold level, whereupon benthic abundance appears to reach a maximum level, further supporting the suggestion of Lampitt and Antia (1997). In the deep north-east Atlantic PAP and BIS sites, benthic polychaete abundance was not as high as predicted if the relationship with production were linear.

An alternative hypothesis is that in the north-east Atlantic PAP area, competition by surface dwelling megafauna is preventing the benefits of enhanced organic input reaching the polychaetes. Thurston *et al.* (1994;1998) have measured megafaunal abundance and taxonomic composition in the north Atlantic. At PAP, surface grazing holothurians dominate, whilst at MAP and EOS, they are conspicuously absent and ophiuroids are the dominant megafaunal taxon. Megafaunal abundance and biomass at PAP are much higher than at MAP and EOS.

This competition hypothesis is not supported, however, by the data on POC flux reported by Lampitt and Antia. Although it is possible that competition is preventing the polychaetes from becoming dominant at PAP, it is more likely that it is the lower than expected POC flux that is the primary cause. The conclusion is that both productivity and benthic abundance may well be good proxies for POC flux at intermediate to low levels of productivity, but at levels of productivity above 200 gCm^{2}yr^{-1}, only benthic abundance is a suitable proxy for POC flux.

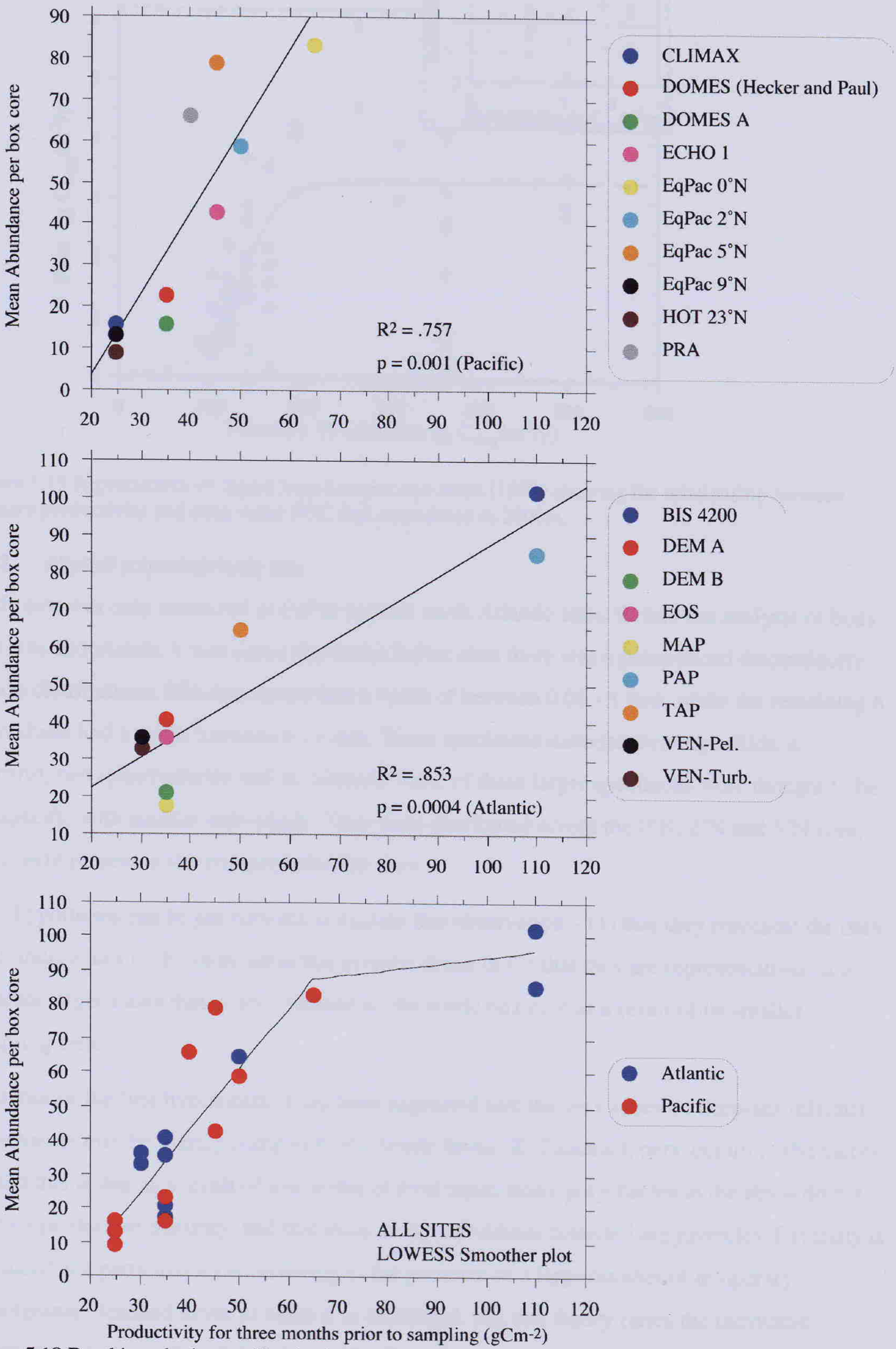


Figure 5.18 Benthic-pelagic coupling in the Pacific and Atlantic oceans, productivity rates estimated from SeaWIFS / Rutgers University Ocean Primary Production Maps. Extra site data obtained from additional publications on DEM-A, B (Sibuet *et al.*, 1984); BIS 4200 (Laubier and Sibuet, 1979); Ven-Pel, Ven-Turb (Richardson and Young, 1987) and CLIMAX (Hessler and Jumars, 1974).

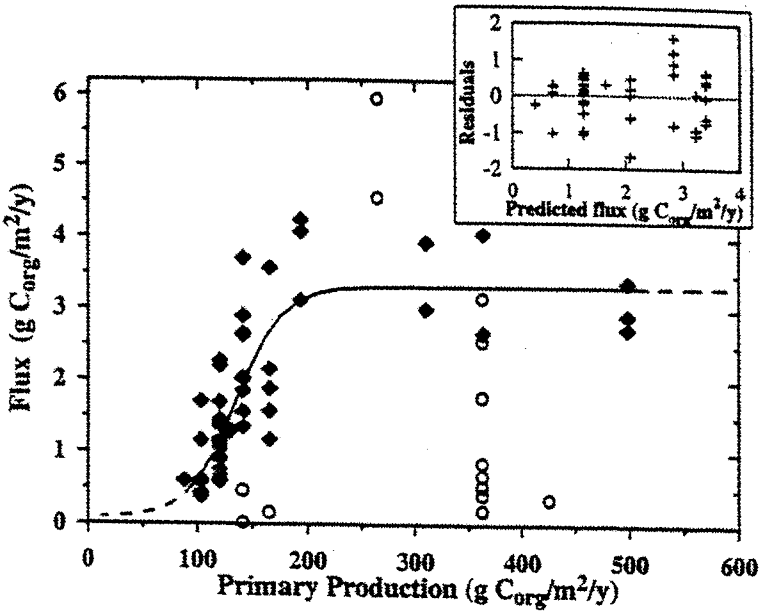


Figure 5.19 Reproduction of figure from Lampitt and Antia (1997) showing the relationship between primary productivity and deep water POC flux normalised to 2000m.

5.3.2 Abyssal polychaete body size

Body size was only measured at EqPac and the north Atlantic sites. Before the analysis of body size was undertaken, it was noted that at the EqPac sites there was a pronounced discontinuity in size distributions. 836 individuals had a width of between 0.06 - 1 mm, while the remaining 6 individuals had a width between 6-17 mm. These specimens included two capitellids, a glycerid, two sphaerodorids and an orbiniid. None of these larger specimens were thought to be conspecific with smaller individuals. They were distributed across the 0°N, 2°N and 5°N sites; none were present at the non-phytodetrital sites.

Two hypotheses can be put forward to explain this observation – (1) that they represent the only adult individuals of the more abundant juvenile fauna or (2) that they are representatives of a separate larger fauna that is not collected by the spade box core as a result of its smaller sampling area.

In favour of the first hypothesis, it has been suggested that the very speciose deep-sea infaunal polychaetes may be mainly composed of juvenile forms (K. Fauchald, pers. comm.). The theory behind this is that as a result of low levels of food input, many polychaetes in the abyss do not reach reproductive maturity, and that most of the individuals collected are juveniles. Diversity is enhanced at a particular location owing to the presence of a large number of temporary 'immigrants' destined never to make it to adulthood. But this theory raises the inevitable question – where are the adults? According to the theory, the adults are so sparsely distributed as to be rarely collected.

A number of lines of evidence lead us to reject this first hypothesis in favour of the second. Firstly, the 'adult' fauna, if it exists, has never been discovered, which is surprising as the adults must match the juveniles in terms of diversity, and be common enough to reproduce to such an extent as to populate the entire deep-ocean with their offspring. Secondly, the tiny infaunal polychaetes, of which the cirratulids, paraonids, spionids and sabellids are the prime examples, contain the full gamut of adult morphological features, and do not appear as shallow-water juveniles do. In other words, although small, they appear like adults. The only exception to this rule is that they have in many cases lost some shallow-water adaptations, and they appear to have far fewer chaetigers. Thirdly, a number of very small deep-sea polychaetes have been collected in enough numbers for studies of growth and reproduction to be made – Blake (1993) studied the size distributions of five dominant infaunal polychaetes from the North Carolina continental slope, and in this study, enough individuals of *Sigambra magnuncus* were obtained for the allometric growth pattern to be observed.

The final and most persuasive argument in favour of the 'separate fauna' hypothesis is that those larger animals that have been collected appear to differ from the small ones at both species and family level. One of the most famous collections of annelids is that of the early oceanographic ship HMS *Challenger*. The large sieve size and primitive sampling methodologies employed on the 19th century vessel meant that only large organisms could be sampled. But there is no evidence to suggest that these specimens are adult representatives of the more common smaller forms found today in box cores. Rather, they appear to differ quite dramatically at a family level (Table 5.5). None of the dominant families in the *Challenger* collection are represented in any number in the box core collections. It seems likely that the larger organisms are fulfilling a quite different functional role on a different scale to the smaller infaunal polychaetes.

Abyssal EqPac sites (box-core)		**HMS *Challenger* (trawls)**	
Family	%	Family	%
Spionidae	19	Terebellidae	14
Cirratulidae	17	Ampharetidae	13
Paraonidae	13	Maldanidae	11
Syllidae	13	Onuphidae	10
Acrocirridae	7	Polynoidae	10
Sabellidae	6	Aphroditidae	9

Table 5.5 Dominant families collected in the abyss from the EqPac box cores compared with those from the trawled collections of HMS *Challenger* (McIntosh, 1885).

The paucity of large polychaetes in the deep ocean, and the enhanced abundance and diversity of tiny sediment-dwelling specimens follows on from the general hypothesis of Thiel (1975), that the higher total metabolic requirement of larger organisms is selected against in the food poor deep sea. But the evidence from the EqPac box-cores, and the *Challenger* material, suggests that although sparsely distributed, these larger organisms are still prevalent in the deep sea. Abyssal studies based only on box cores may miss many of these larger specimens.

5.3.3 The effect of phytodetrital food input on body size

A conspicuous feature of deep-sea macrofaunal invertebrate species is their small body size (Gage and Tyler, 1991; Rex and Etter, 1998; Rex *et al.*, 1999). But the explanations for the cause of this pattern are not obvious. The deep-sea is a food-limited environment, and it is well known that organisms with larger body sizes are more metabolically efficient, and require less food per unit of mass (Rex and Etter, 1998). Hence one might suppose that deep-sea organisms should in fact be larger than their shallow-water counterparts.

In fact, the assertion that deep-sea invertebrates are universally small is false – some invertebrates actually do show a trend towards 'gigantism' in the deep sea. One of the more famous examples is the giant scavenging amphipod *Eurythenes gryllus* (Gage and Tyler, 1991). Some species show a trend for increased appendage length, such as in the aselote isopod *Munnopsis longiremis*; by increasing the length of appendages, the organisms can occupy a larger ambit without needing to increase total body mass considerably. Recently, Rex *et al.* (1999) have reported that for deep-sea gastropod species, body size also increases with increasing depth.

Explanations for the bathymetric trends revolve around food availability, which is assumed to decrease with increasing depth. It has been suggested that body size is the result of two processes – (1) an ecological trade off between metabolic efficiency (favouring largeness) and the difficult of maintaining reproductively viable population sizes (favouring smallness and increased abundance) and (2) phylogenetic constraints (e.g. nematodes are smaller than polychaetes for historical – phylogenetically constrained reasons).

In this study, the largest polychaetes were found at the most food impoverished sites (Figures 5.9, 5.13, 5.16). In the north Atlantic individuals of all the dominant families were smaller at food rich sites, in the central Pacific, the relationship was less strong, but still apparent for some of the families. This was also tested at a within species level for some of the cosmopolitan species of the north Atlantic, which showed a similar trend to reduced body size at the food rich PAP site (Figure 5.15).

This result is in complete contrast to the pattern found at the same EqPac sites for the nematode fauna (Brown *et al.*, in press). Brown *et al.* found the opposite - nematodes were significantly larger in phytodetrital sites than in non-phytodetrital sites. Admittedly, for polychaetes, the pattern at EqPac is not as clear as it is in the north Atlantic, but for certain families the general trend is still apparent. Brown *et al.* attributed the increased size at the food rich sites to the increased availability for food and hence, following the hypothesis of Thiel (1975), larger organisms are able to survive as they can fulfill their larger energetic demand.

Rex *et al.* (1999) have shown how different groups of organisms may respond differently in terms of body size. The increase in gastropod body size with depth indicates that these species, in common with the polychaetes in this study, may be reduced in size (although more abundant) with increasing food availability. A suitable hypothesis exists to explain this pattern – at larger body sizes, individuals become metabolically more efficient. In other words, less food is required for each unit of body mass in larger individuals. To explain why body size should *decrease* with decreasing food availability, Thiel (1975) suggested that this advantage of metabolic efficiency must be counteracted by other factors – namely the problem of maintaining a minimum viable population.

Some caveats must be applied to the analysis of polychaete size distributions. Rex and Etter (1998) indicated that for a valid comparative analysis of body size to be undertaken, two important factors must be accounted for. The first is that pooling an entire group of organisms (such as the polychaetes) and comparing their mean body size may be invalid if families or species within that group are responding differently in terms of their body size. This problem has been effectively answered by the analysis within families (Figures 5.9 and 5.14) and where possible, within species (Figure 5.15). The second problem is that a one-off analysis of body size may be a reflection of the recent history of recruitment and population growth, which we now know can be seasonal or unpredictable for some deep-sea species (Gage and Tyler, 1991). This second caveat is more problematical – one potential reason for reduced body size at PAP is that the samples were taken following a reproductive period, and that many of the individuals are young adults or juveniles. Against this argument it was observed that for some of the PAP box cores (which were sampled at a different time of year) there was no significant difference in body size before or after the summer bloom event, when a reproductive pulse might be expected. In fact, there is very little evidence for reproductive periodicity in deep-sea polychaetes from any other studies, based on analyses of size distributions (Hartman, 1965; Blake, 1993). In addition, a recent study by Ambrose and Renaud (1997) showed that even in the shallow-water polynya of Antarctica, which receive a highly seasonal input of food, there was no evidence to suggest that the polychaetes might be reproducing seasonally in response to this. It must remain a possibility that there is seasonal recruitment at the phytodetrital sites, but other studies suggest that it is unlikely.

A final hypothesis to explain the reduced polychaete body size at the phytodetrital sites is that of competition. At PAP, megafaunal abundance is much higher than at MAP or EOS (Thurston *et al.*, 1994; Thurston *et al.*, 1998). Furthermore, at PAP, there is a much higher proportion of potentially bioturbating organisms such as large holothurians and burrowing echiurans. It is possible that these larger megafauna are utilising a larger proportion of incoming food and limiting the amount available to the polychaetes. Alternatively, it is the enhanced abundance of the polychaetes themselves that are generating greater intra-specific competition for resources. It is difficult to isolate causal variables from a network of coexisting patterns.

In summary, abductive inference generates three potential hypotheses to explain the observed pattern. Firstly, polychaetes are smaller at food rich sites as a result of reduced requirements for metabolic efficiency through large body size. Secondly, that it may be an artifact of a seasonal recruitment event, and finally that inter and intra-specific competition at the more populated food rich sites prevents the polychaetes from growing to the sizes found in the less densely populated sites.

One further piece of evidence supports the hypothesis that the relationship is based on food availability, and not a seasonal recruitment pattern. That is, polychaetes are larger in the deeper layers of the sediment (Figures 5.10, 5.11). At the EqPac sites, where depth profiles were available, all families of polychaetes were larger in the deeper layers of the sediment, where food is more scarce. Although this might reflect phylogeny – certain species may be phylogenetically constrained to live within the sediment (see chapter 4, where it was shown that cirratulids show precise vertical profiling) – it is apparent that even for species which were abundant throughout the sediment, they showed reduced size at the surface (Figure 5.11).

These observations of vertical profiling support the hypothesis that it is a question of metabolic efficiency trade-offs – in that in the food poor deeper layers, it is more efficient to have a larger body size. Alternatively, the data could also support the hypothesis of competition, which is reduced in the deeper layers of the sediment, where polychaetes are less abundant, as are their potential competitors for food, the megafaunal grazers.

Rex *et al.* (1999) concluded that:

> *"The adaptive significance of body size is a problem of fundamental and growing interest in evolutionary ecology..."*

This study has shown how body size may well be influenced on small, local ecological scales as well as larger macroevolutionary ones. Patterns in polychaete body size are closely related to patterns of food availability. Teasing out the relative significance of energy requirement trade-offs, seasonal recruitment and competition will require further work.

5.3.4 Concluding remarks on benthic-pelagic coupling in the abyssal ecosystem

The recent discovery of a long-term change in the abyssal megafauna of the north-east Atlantic (the so-called '*Amperima* event') has revealed that an understanding of the ecological dynamics of the abyssal ecosystem is far from complete (D. Billett, R. Lampitt, pers. comm.). The dramatic increase in abundance of the megabenthic holothurian *Amperima rosea* is not well correlated with any of the currently measured variables. Ecological theory is frequently foundered in the face of such surprising observation. Much of deep-sea ecology is still at such a position – that of conjecture in the face of a new and surprising fact.

The polychaetes exhibit marked variation in both abundance and body size across the abyssal ecosystems of the world. At the EqPac site, polychaete abundance drops sixfold over a distance of just 400km. Variation in the levels of new production in the surface waters over 4 km above the bottom seems to explain over 70% of this variability in when both the Atlantic and Pacific ocean datasets are combined. In the far north-east Atlantic, at the well-studied Porcupine Abyssal Plain site, surface production is amongst the highest in the world, yet only a tiny fraction of this productivity is reaching the seabed, and it appears to be a smaller fraction than that for most of the other sites in the abyss, given the observed levels of abundance.

The polychaetes are responding to these changes in food availability both in terms of abundance and in body size; very small scale changes in the body size of the dominant components of the polychaete fauna provide clues to adaptive processes in the deep sea. Understanding patterns in body size on a macroevolutionary scale may be important in terms of biodiversity; but the large-scale patterns require an understanding of small scale patterns first. At present, it is not possible to separate potential adaptive reasons for observed patterns in body size to those generated by competition or reproduction.

There is clearly a need for time-series data on deep-sea polychaetes, especially in areas that receive seasonal and interannual variations in food input, as is the case at the EqPac and PAP sites. This would resolve a number of these questions regarding the nature of the benthic-pelagic relationship. There is some limited evidence from EqPac that the polychaetes may be responding quite quickly to the input of phytodetritus, as the abundances are explained best by production when values for the preceding three months are used, rather than the average for the entire year. Time-series data would resolve whether: (1) polychaetes have a characteristic response-time to an influx of new food; (2) whether they exhibit a reproductive pulse following this food input; (3) if a seasonal input of phytodetritus selects for smaller body sizes, or whether this is a response to increased competition and (4) whether there is a difference in life-history strategies between sites receiving a temporally variable high input of food and sites receiving a steady year-round rain of food particles.

6 SPECIES DIVERSITY OF ABYSSAL POLYCHAETES

> *"I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject) as soon as facts are shown to be opposed to it... I cannot remember a single first formed hypothesis which had not after a time to be given up or greatly modified."*
>
> *- Charles Darwin*

6.1 Introduction

It will be recalled from section 2.4 that, given the current state of background knowledge, a number of obvious hypotheses suggests themselves with regard to species diversity in the abyss. Firstly, that species diversity will be higher under higher productivity regimes, secondly that it will be related to the patchy nature of food input at phytodetrital sites, thirdly that it will be influenced by both large and small scale disturbance and finally that diversity at a particular point (alpha diversity) will be enhanced by regional diversity. Some questions also arise regarding the patterns of beta diversity, but considering the limited amount of research that has gone on in this area, only specific questions, rather than testable hypotheses can be pursued.

There is variability enough to test these hypotheses of alpha diversity in the 12 sites that are investigated - food input is variable; it occurs in a patchy nature at PAP and EqPac; small-scale disturbance is higher at PAP and EqPac; large-scale disturbance is highest at MAP; finally, regional diversity is potentially much higher in the Pacific than in the Atlantic.

A number of deep-sea workers have already reported links between species diversity and productivity. Firstly, there is the bathymetric species diversity gradient, established for gastropod molluscs by Rex (1973; 1976; 1981), macrofauna by Blake *et al.* (1987) and polychaetes by Paterson and Lambshead (1995). Given that food availability has generally been shown to decline with increasing depth (Gage and Tyler, 1991), it has been invoked as the causal variable (Huston, 1979; Rosenzweig and Abramsky, 1993). Cosson-Sarradin *et al.* (1998) have reported a close link between deep-sea polychaete diversity and the nature of organic inputs off the west African upwelling system.

More relevant to this study is the recent work of Brown (1998) on nematodes from the EqPac transect. She found that species diversity of the nematode fauna was enhanced at the phytodetrital EqPac sites, attributing the pattern principally to the increased spatial heterogeneity of food resources at these sites. This raises the question of whether it is the productivity *per se* that is enhancing diversity (a larger cake; a longer stick) or whether it is the variables associated with this enhanced productivity – such as the patchiness of food input. Evidence from theoretical and empirical ecology suggests that both an increase in nutrients on their own, and the patchy nature of food availability may increase diversity. An increase in resources permits the existence of more rare species, following the premise of Preston (1962), as observed by Rosenzweig (1995). At the same time, spatio-temporal patchiness of resources permits the existence of a mosaic of succesional states, as predicted by Grassle and Morse-Porteous (1987). In a review, Grassle (1989) has suggested that '*...organic particulate matter settling to the bottom is a major source of spatial and temporal heterogeneity*' and that such patchiness of organic inputs is a major factor in the maintenance of species diversity in an otherwise homogenous environment.

There have been some studies designed specifically to test this hypothesis, prior to that of Brown (1998). Rice and Lambshead (1994) have observed the higher diversity of nematodes at the phytodetrital PAP site compared with the non-phytodetrital MAP site. In contrast, Paterson *et al.* (1998) discovered no differences in diversity between the PAP site and the non-phytodetrital EOS site.

Difficulties in understanding the productivity-diversity relationship in the deep north Atlantic may be attributable to terrigenous influences. As outlined in section 1.4, the MAP site lies in a region of large-scale physical disturbance caused by a turbidite emplacement. The EOS site lies close to the west African upwelling zone; interannual variability in particle flux may be a factor at this site (see Figure 5.2). One of the major goals of this study was to investigate whether the productivity-diversity relationship was more obvious in the EqPac location than in the more complex north-east Atlantic.

Understanding the scale of diversity being measured is probably more important in deep-sea ecology than in any other ecological discipline. The current trend towards macro-ecological studies, such as the latitudinal diversity gradient, reinforces the need to be clear as to the pattern, and the questions that can be addressed with it. Recent studies have focussed on such large-scale questions (Rex *et al.*, 1993; Rex *et al.*, 1997; Rex *et al.*, 2000); yet other authors have argued that these large-scale patterns may be best explained using small-scale processes (Gray, 1997; Gray, 2000; Lambshead *et al.*, 2000). Crucial to understanding large-scale patterns of diversity is the degree of faunal turnover, or beta diversity.

Beta diversity has been variously described as the slope of the species-area curve (Rosenzweig, 1995) and the degree of change in species composition along a gradient (Whittaker, 1960; Gray, 2000). In reality, the former is a function of the latter. In deep-sea studies, sampling design limits an investigation of species-area curves, terrestrial-style. A simple index of similarity between samples and sites is more appropriate.

The degree of faunal turnover between sites, and on an even larger scale, the similarity of the fauna across ocean boundaries, has evolutionary as well as ecological implications. The Pacific Ocean, with its greater age and larger size, has a higher level of regional diversity than the Atlantic. High regional diversity can influence local, alpha diversity (Ricklefs, 1987; Cornell, 1993), hence it can be hypothesised that alpha diversity will be higher in the Pacific than in the Atlantic.

In summary, this study compares directly, for the first time, the productivity-disturbance and diversity pattern in the abyssal sites of the Pacific and north Atlantic. This analysis permits an investigation of both the relationship between alpha diversity and local processes, as well as an investigation of regional beta diversity patterns and the potential total biodiversity of the abyssal ecosystem.

6.2 Results

Table 6.1 summarises the number of species and the number of individuals from each site. The greatest number of species were recorded from the ECHO 1 site, and the smallest number of species from the HOT 23°N site. The manganese nodule sites are the most intensively sampled, and the HOT 23°N site is the least intensively sampled.

Site	Position	Depth	No. of Individuals	No. of Species	No. of Samples
EQPAC 0°N	0°N 140°W	4300m	175	73	3
EQPAC 2°N	2°N 140°W	4400m	163	82	4
EQPAC 5°N	5°N 140°W	4400m	167	76	3
EQPAC 9°N	9°N 140°W	4900m	28	23	3
HOT 23°N	23°N 158°W	4800m	18	14	4
DOMES A	8°27'N 150°47'W	~5000m	752	104	47
PRA	12°57'N 128°19'W	4800m	1043	100	15
ECHO 1	14°40'N 126°25'W	4500m	634	113	15
PAP	48°N 16°W	4800m	427	101	5
TAP	38°N 11°W	5035m	186	57	8
MAP	31°N 21°W	4900m	87	29	5
EOS	20°N 30°W	4600m	214	75	6

Table 6.1 Summary information on the number of individuals and number of species from each of the 12 abyssal sampling sites.

In the following sections the patterns of species diversity are explored at a scale of point diversity (individual box cores), alpha diversity (pooled box cores from a sampling station) and beta diversity (change in species composition across sites). Finally, taxonomic composition is analysed to see if changes in species composition can be related to environmental variables. The methods used to estimate species diversity are all to a greater or lesser extent influenced by equitability, simple counts of the number of species are unsuitable because of variation in sampling intensity between sites (as indicated in Table 6.1).

6.2.1 Species diversity indices

Variability in point species diversity index values (Shannon H' and Simpson *D*) is explored in Figure 6.1. Point diversity was highly variable when the Shannon H' measure of diversity was used, but there was little or no variability in the values of Simpson *D*. The Shannon H' index is more sensitive to species richness and the Simpson *D* index is more sensitive to equitability.

Theoretically, Simpson *D* may vary from 0 (maximum evenness) to 1 (maximum dominance). The low variability in Simpson's index is indicative of a high level of evenness at all sites; the wide variation in Shannon H' is indicative of variability in species numbers, caused either by genuine changes in species richness, or by density-dependence as a result of the variability in abundance observed in Chapter 5. H' is lowest at the HOT 23°N site, and highest at the EqPac 0°N site. H' was highest at the phytodetrital sites (black filled circles). In the north Atlantic, H' was lowest at the MAP site. In the equatorial Pacific, H' was lowest at the HOT 23°N, EqPac 9°N and DOMES A sites.

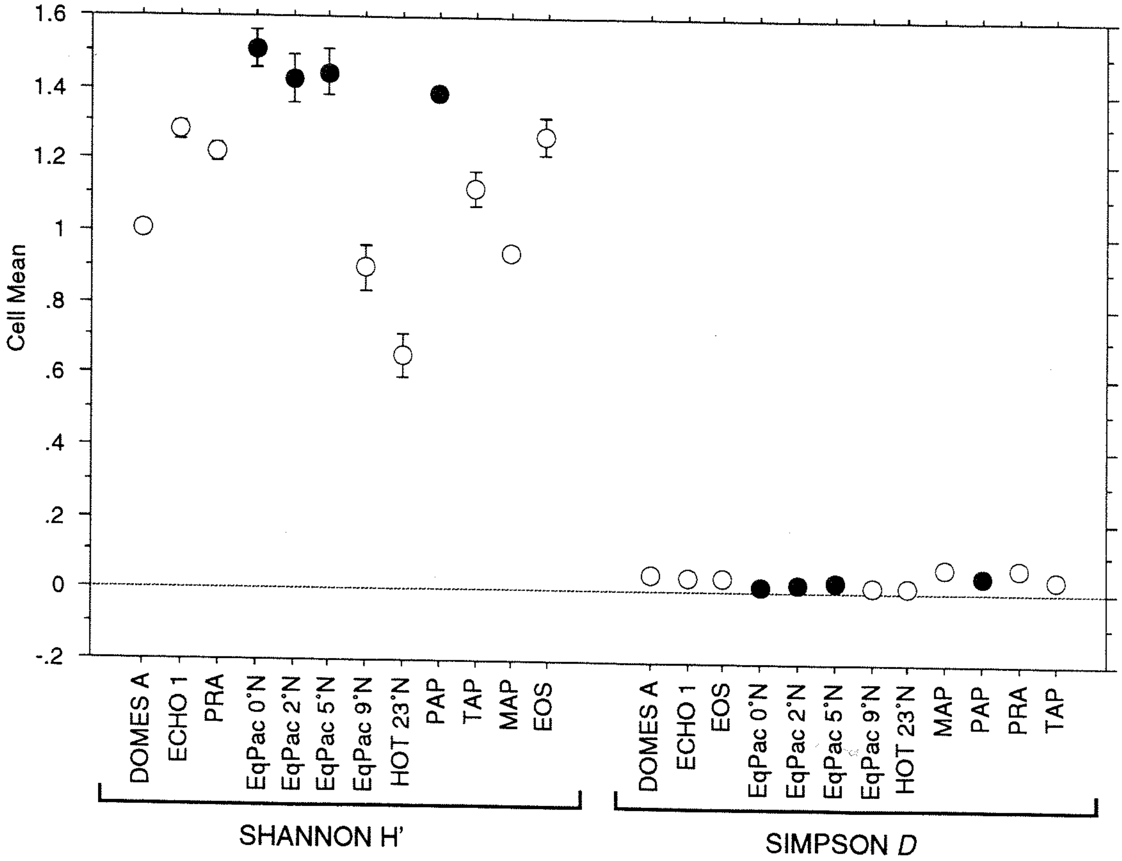


Figure 6.1 Shannon H' and Simpson D for individual box cores (mean values). Error bars are ± 1S.E. Black filled circles are those sites that receive phytodetrital input.

Variation in point diversity and alpha diversity, as measured using Shannon H', was explored in further detail at the EqPac and HOT 23°N site (Figure 6.2). Diversity was highest at the EqPac phytodetrital sites, lower at the 9°N site, and lowest at the HOT 23°N site. The same pattern was observed for point diversities of box cores, and diversity of pooled box cores (alpha diversity). The point diversities were correlated strongly with POC flux to the sea bed, with the high POC flux EqPac phytodetrital sites having the highest diversity.

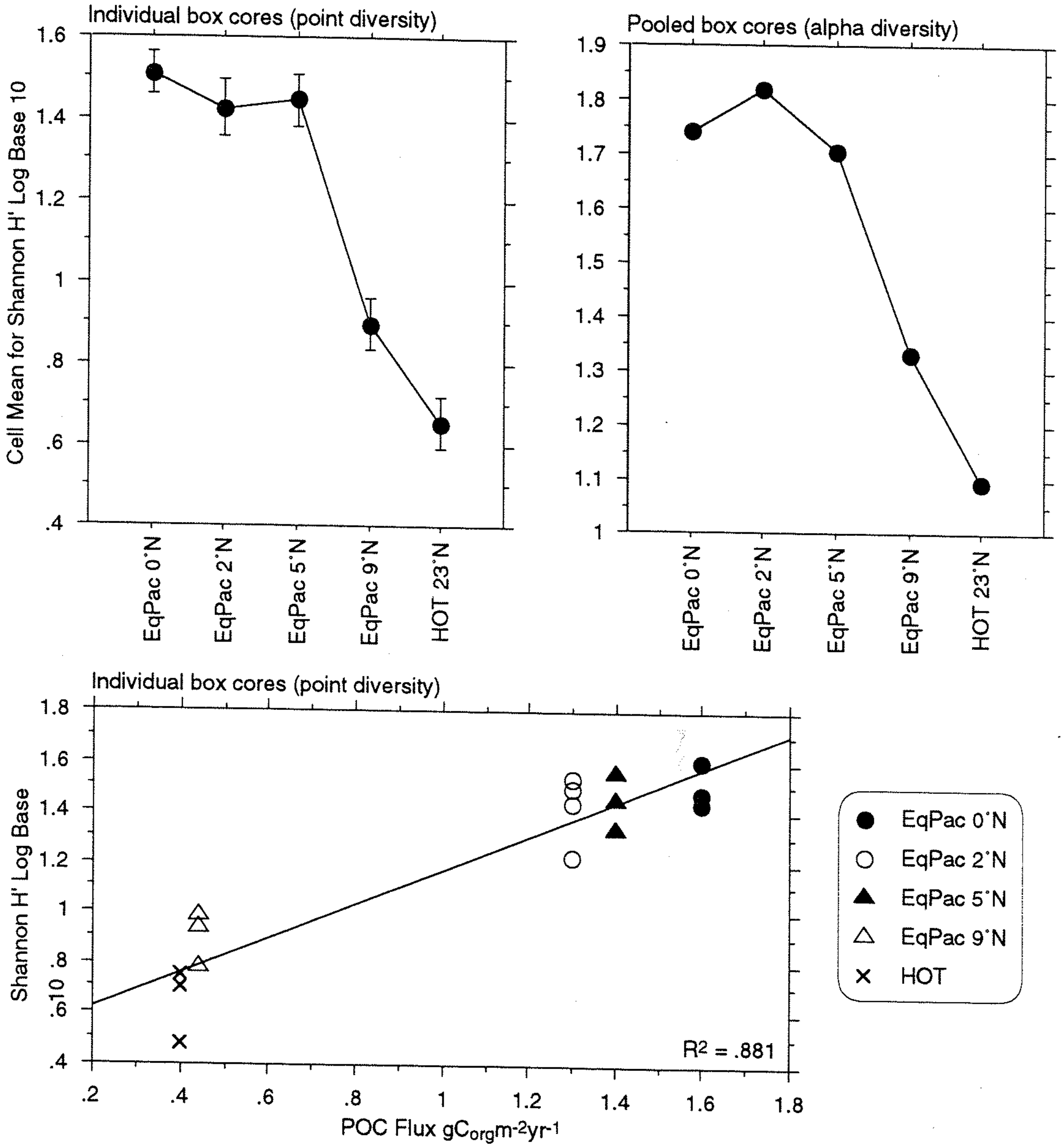


Figure 6.2 Shannon H' diversity at the EqPac and HOT 23°N sites, showing the relationship between organic carbon flux and alpha diversity of abyssal polychaetes. Error bars are ±1S.E.

A potential problem with the Shannon H' diversity measure is density-dependence. Simpson *D*, a relatively density independent measure, was similar at all the abyssal sites. In contrast, H' is highly variable. A potential cause of the variability in H' is density-dependence. The density-dependence of H' is explored in Figure 6.3. Two regressions have been performed on the data, one of diversity in box cores with less than 35 individuals (regression line 1, open circles) and one on box cores containing more than 35 individuals (regression line 2, filled circles). The cut-off point of 35 individuals was chosen as this was the area of the plot where there appeared to be the most abrupt change from density-dependence to density independence. There is considerable density-dependence of H' in the low abundance box cores, with abundance explaining 57% of the variation in H'. In box cores containing more than 35 individuals, very little of the variation in H' is explained by abundance, and H' is relatively density-independent.

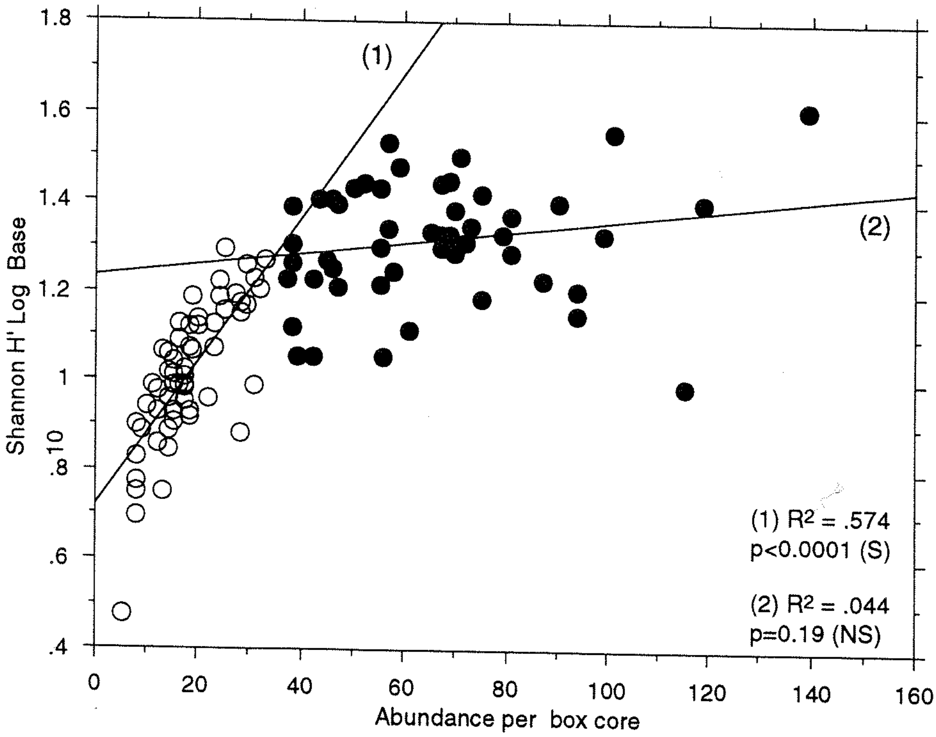


Figure 6.3 Density-dependence of Shannon H'. Regression line (1) based on open circles for box cores with less than 35 individuals, regression line (2) based on filled circles for box cores with more than 35 individuals. 'S' denotes significance at the $p<0.05$ level, 'NS' denotes non-significance.

The high density-dependence of H' in low abundance box cores casts doubt on the validity of using H' as a measure of point diversity at some sites. In Figure 6.4, mean values of H' are indicated for samples where more than 35 individuals were collected. Variability in species diversity is still apparent, with the highest richness at the phytodetrital sites (black filled circles) and the lowest at the non-phytodetrital sites (open circles). The table of t-test significance given in Table 6.2. There is only weak support for a phytodetrital effect in the north Atlantic, with no significant differences between the EOS and PAP sites. In the central Pacific, the PRA site has significantly reduced diversity compared to all the EqPac phytodetrital sites although the ECHO 1 site is only significantly different from EqPac 0°N.

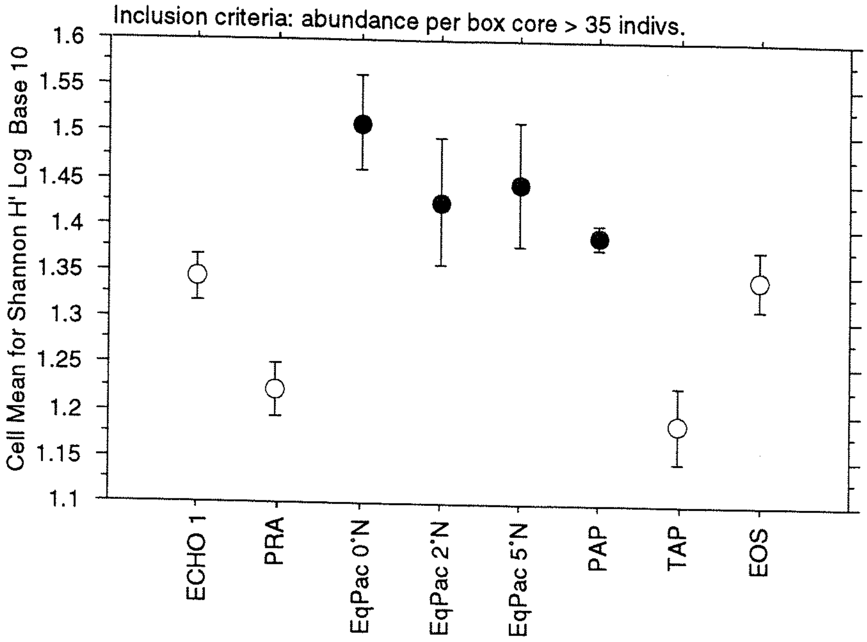


Figure 6.4 Shannon H' at abyssal sites where box cores contained more than 35 individuals. Error bars are ±1S.E.

	ECHO 1	EOS	EqPac 0°N	EqPac 2°N	EqPac 5°N	PAP	PRA
EOS	NS	-	-	-	-	-	-
EqPac 0°N	*	*	-	-	-	-	-
EqPac 2°N	NS	NS	NS	-	-	-	-
EqPac 5°N	NS	NS	NS	NS	-	-	-
PAP	NS	NS	NS	NS	NS	-	-
PRA	**	*	**	**	**	*	-
TAP	*	NS	**	**	**	*	NS

Table 6.2 Table of significance (t-test) for Shannon H' data in Figure 6.6. NS = not significant; * = $p<0.05$, ** = $p<0.01$.

6.2.2 Probabilistic measures of diversity

Given the potential for density-dependence of Shannon H', and the very limited variability of Simpson D at low sample sizes, the rarefaction methodology is applied here as the main method of estimating species diversity. Rarefaction, as with the species diversity indices, is influenced strongly by both species richness and equitability, although it is apparent from the measures of Simpson D in section 6.2.1 that most of the variability in diversity is generated by differences in species richness and not equitability. The sample-size independence of the rarefaction method has been evaluated in Figure 6.5. $E(S_{30})$ is not influenced by polychaete abundance.

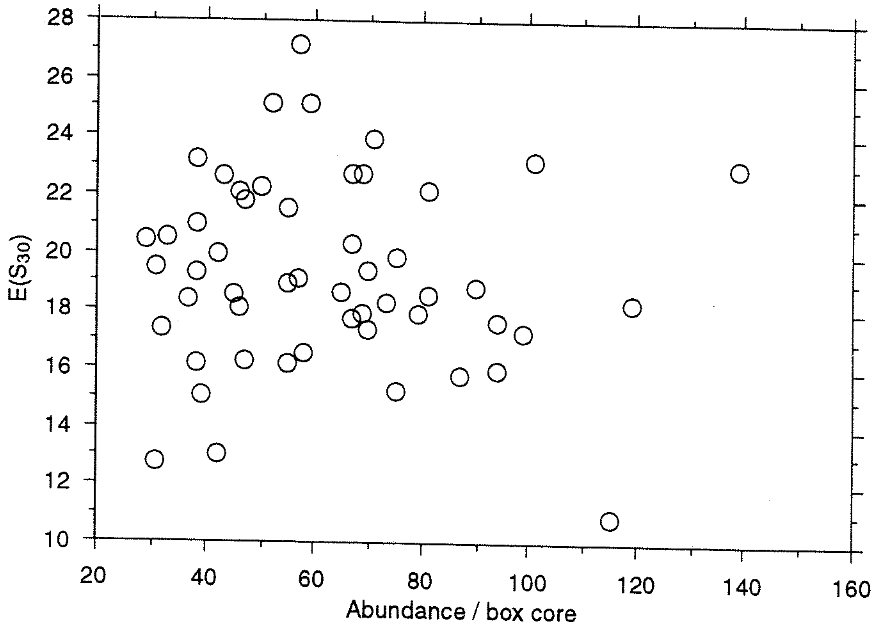
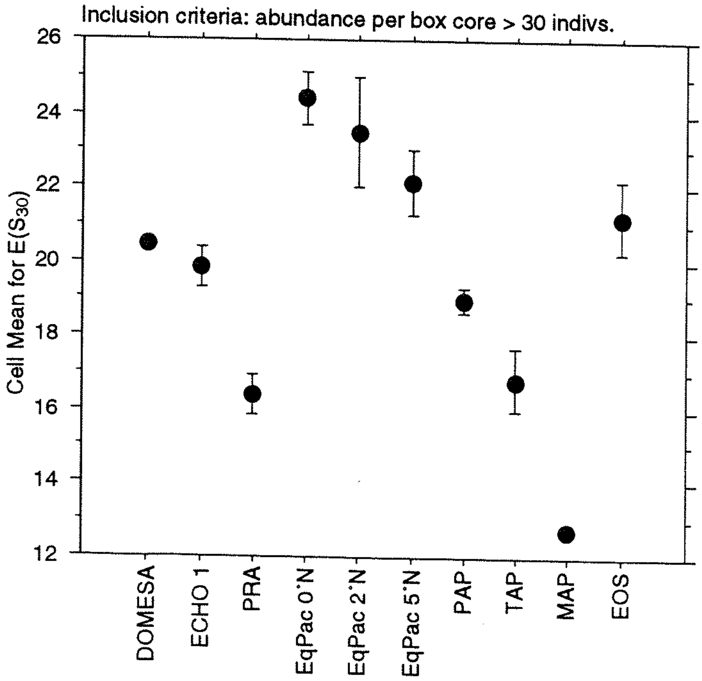


Figure 6.5 Sample size independence of the rarefaction method.

$E(S_{30})$ has been used as an estimate of species diversity in all box cores where at least thirty individuals are present (Figure 6.6). The highest point diversity was found at EqPac 0°N, with a mean $E(S_{30})$ of 24.4, and a lowest level at MAP with a single value of 12.8. There were not enough individuals at HOT 23°N for diversity to be estimated at that site.

In the equatorial Pacific, the phytodetrital EqPac sites have higher point diversities than the non-phytodetrital manganese nodule sites. In the north Atlantic, this pattern is not observed, with the non-phytodetrital EOS site having a higher level of species diversity than the phytodetrital PAP site. The MAP site has low levels of diversity, given that in all other respects apart from the turbidite, the MAP environment is very similar to that at EOS. The TAP site lies midway between the PAP and MAP sites.



	Mean	Count
$E(S_{30})$, Total	19.2	51
$E(S_{30})$, DOMESA	20.5	1
$E(S_{30})$, ECHO 1	19.8	12
$E(S_{30})$, EOS	21.2	4
$E(S_{30})$, EqPac 0'N	24.4	3
$E(S_{30})$, EqPac 2'N	23.5	4
$E(S_{30})$, EqPac 5'N	22.1	3
$E(S_{30})$, MAP	12.8	1
$E(S_{30})$, PAP	19.0	5
$E(S_{30})$, PRA	16.4	16
$E(S_{30})$, TAP	16.8	2

Figure 6.6 $E(S_{30})$ rarefaction estimate of species diversity for thirty individuals; mean values and number of samples provided. Error bars are ±1S.E.

One way of increasing sample sizes is to pool samples from within a site, assuming that all the samples come from the same habitat. Many authors regard species diversity from a particular site as 'alpha diversity', even if it incorporates some aspects of beta diversity in terms of species replacement between box cores. In Figure 6.7, rarefaction curves for individual box cores are plotted, in order to evaluate the suitability of pooling samples. The majority of box cores from sites have very similar rarefaction curves, although at the PRA site, two cores are markedly reduced in diversity compared to the remaining 13. All of the EqPac phytodetrital samples are plotted on the same graph in order to evaluate the suitability of pooling samples from all of these cores.

The rarefaction curves for the pooled samples (Figure 6.8) indicate the potential for high species diversity in the abyss, with none of the curves showing signs of reaching asymptote. In the uppermost graph of Figure 6.8 the entire curves are plotted, in the lower graph, they are plotted only up to the knot size (individual number) of 88, which is represented by the smallest sample, MAP. $E(S_{88})$ values are highest at the phytodetrital EqPac 2'N site (57), and lowest at the north Atlantic MAP site (29), as was the case for the $E(S_{30})$ and Shannon H' analyses. Again, confounding the trend of the Pacific, the non-phytodetrital EOS station has slightly higher diversity than the phytodetrital PAP site.

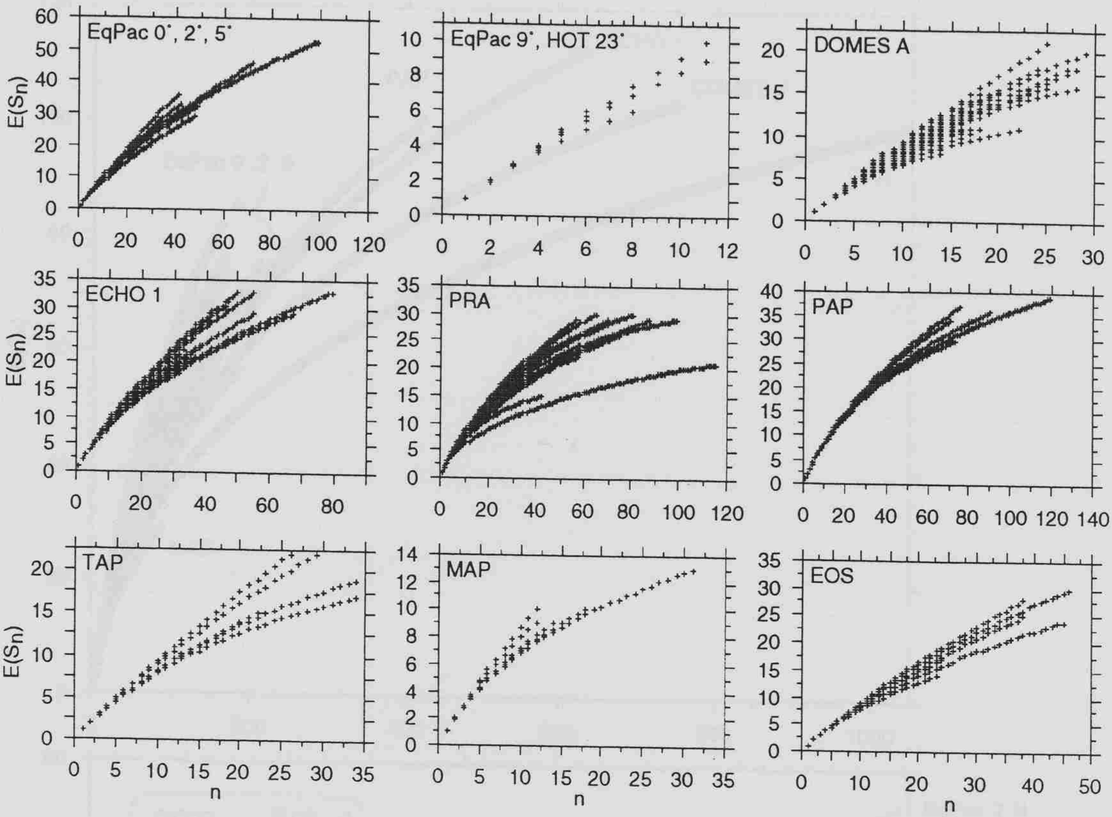


Figure 6.7 Complete rarefaction curves for individual box cores at all abyssal sampling stations. n = no. of individuals.

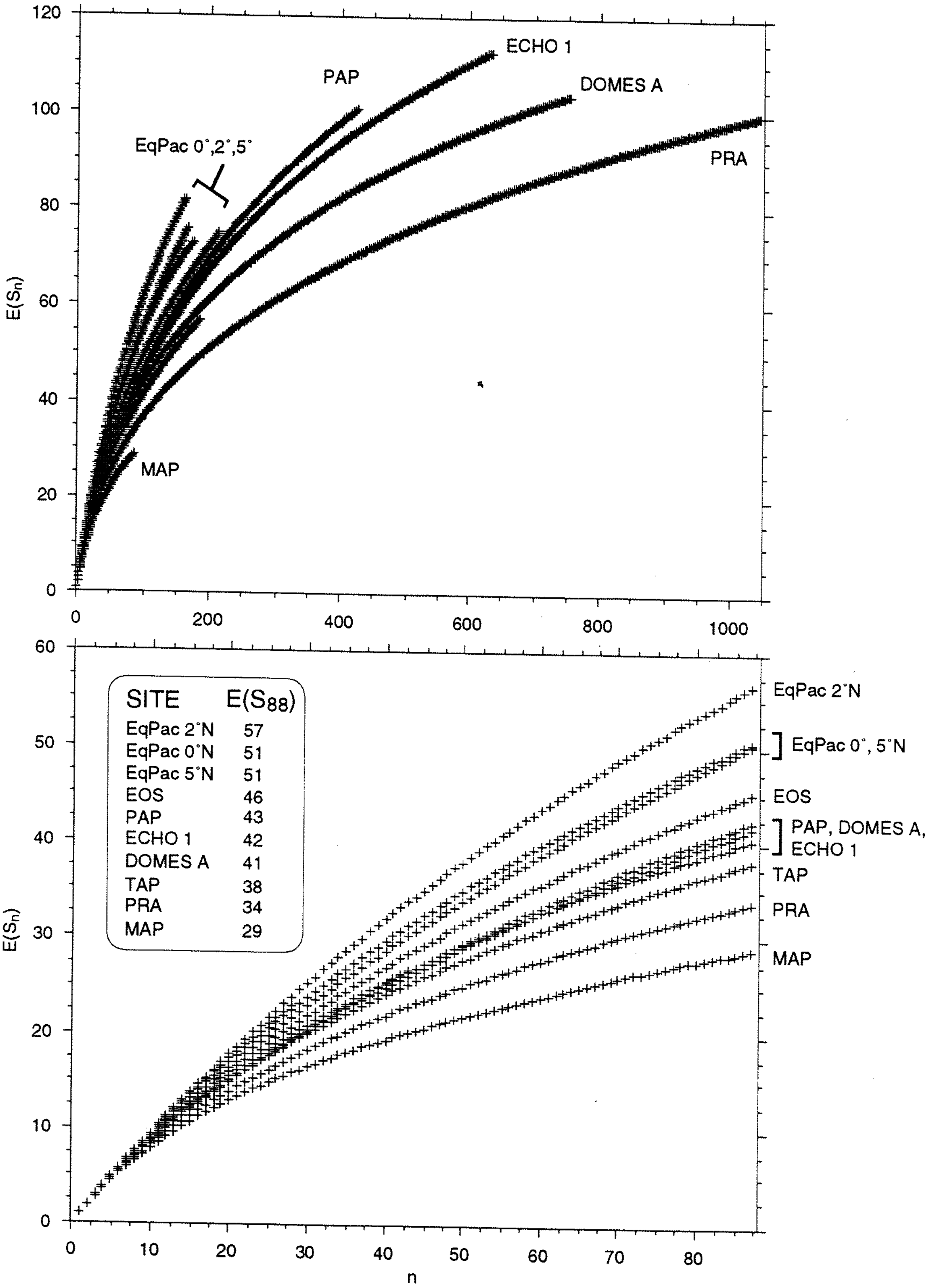


Figure 6.8 Rarefaction curves for sites based on pooled box core samples.

For a direct comparison of the phytodetrital EqPac sites and the non-phytodetrital Pacific sites, samples from all of the EqPac phytodetrital sites were pooled (Figure 6.9). There is a potential for some enhancement of diversity given that the EqPac phytodetrital sites are several hundred km apart. This is because there may be some element of beta diversity, or species turnover, on these larger scales. Even so, diversity at the phytodetrital sites is much higher than at the low productivity sites lying in the oligotrophic gyre regions. At a level of 505 individuals, there are an estimated 147 species at EqPac, 103 at ECHO 1, 90 at DOMES A and 76 at PRA. Diversity is 30 to 50% lower at the non-phytodetrital sites. Diversity has not been estimated at the EqPac 9°N and HOT 23°N sites as there are not enough individuals for a valid comparison.

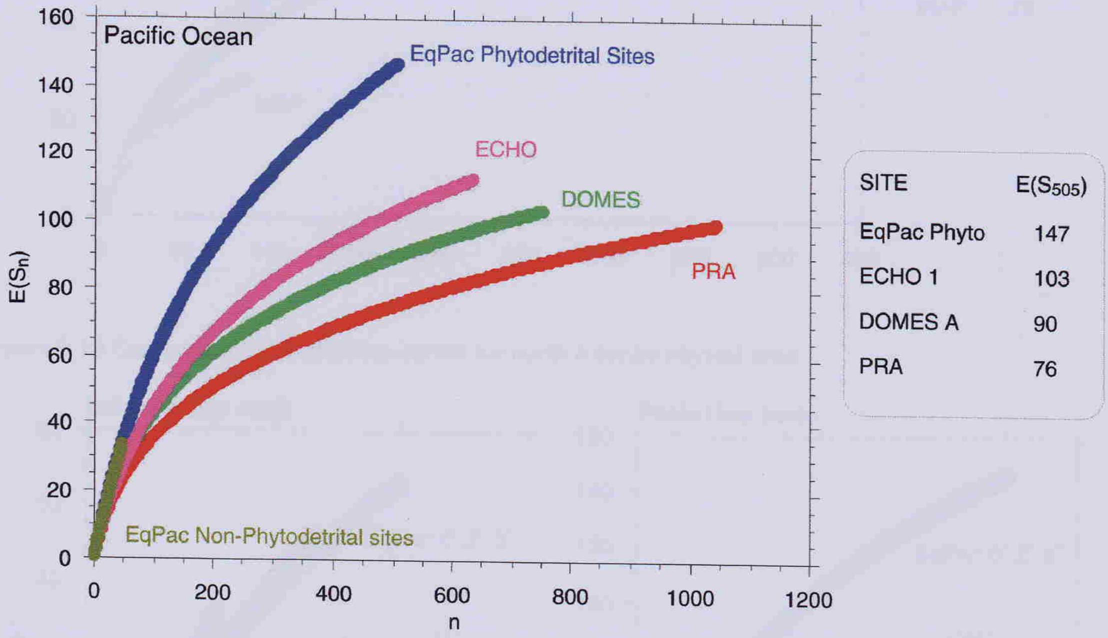


Figure 6.9 Comparison of rarefaction curves for pooled EqPac phytodetrital sites and non-phytodetrital manganese nodule sites.

In the north Atlantic (Figure 6.10), rarefaction curves for the EOS and PAP sites are very similar, while diversity is slightly reduced at TAP, and MAP has the lowest diversity. At a level of 87 individuals, there are an estimated 45 species at EOS, 43 at PAP, 38 at TAP and 29 at MAP. The very low diversity at MAP is in agreement with the results from the individual box cores and Shannon H' analyses.

For a valid comparison between Atlantic and Pacific diversity, the PAP and EqPac phytodetrital sites were selected. Both sites lie under high productivity regimes, experiencing a spatio-temporal patchiness in phytodetrital fall and food availability. Both are regions where small-scale disturbance is prevalent, caused by bioturbating megafauna. Finally, enough individuals are present at both sites for a robust rarefied sample to be taken. Figure 6.11 shows a comparison of rarefaction curves for both individual (left-hand graph) and pooled samples (right-hand graph). In both cases, diversity is higher at the EqPac sites than at the PAP site.

When the pooled values are analysed, 136 species are estimated from 427 individuals at EqPac, and 101 species from the same number of individuals at PAP.

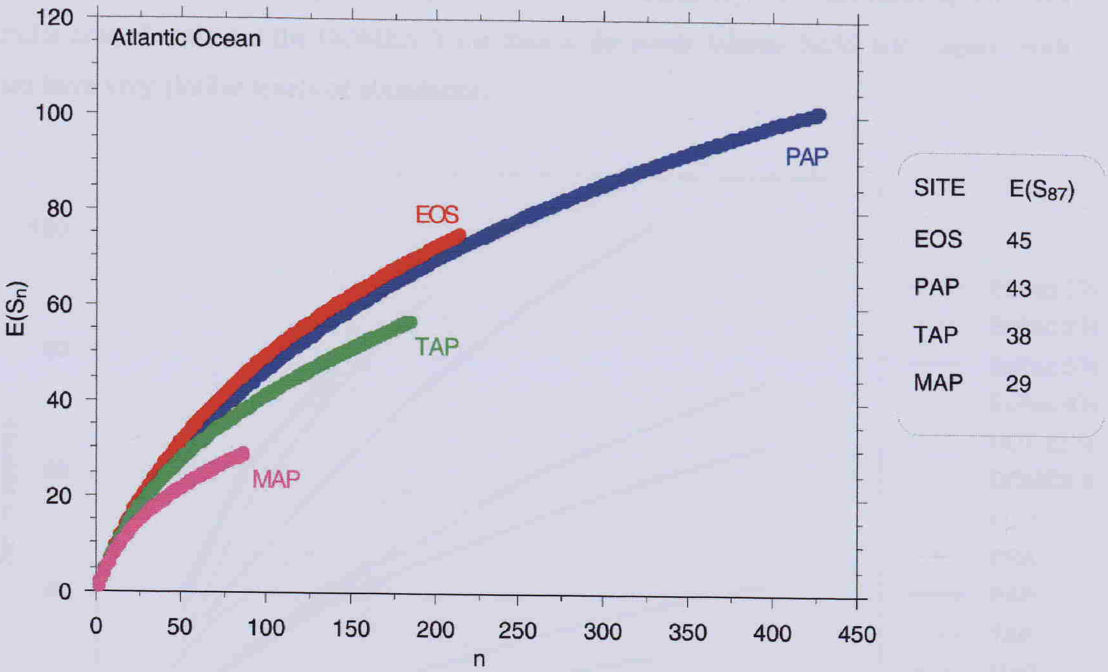


Figure 6.10 Comparison of rarefaction curves for north Atlantic abyssal sites.

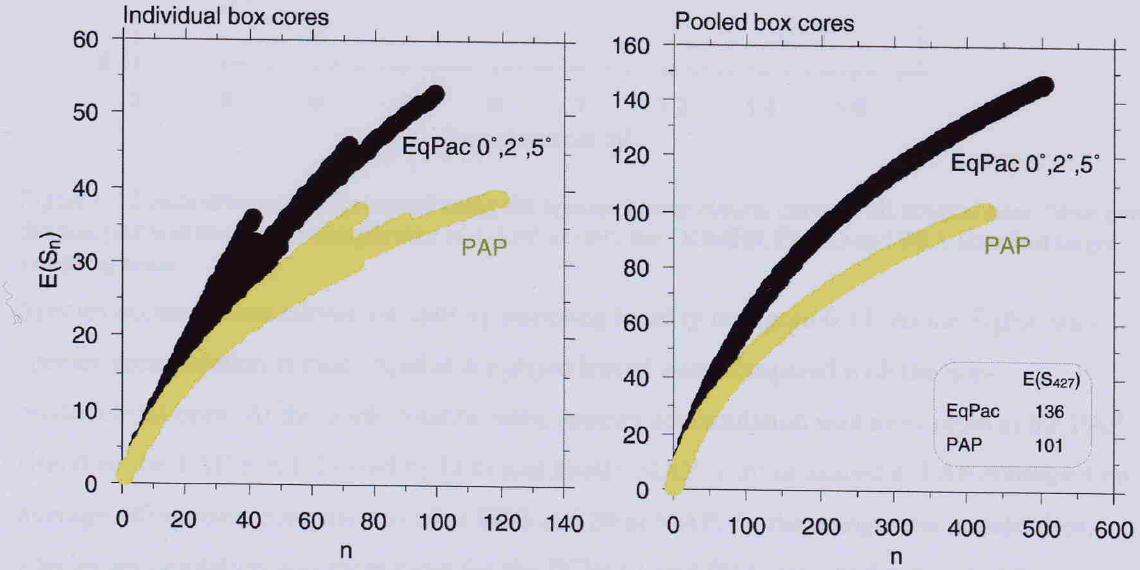


Figure 6.11 Comparison of alpha diversity between Atlantic and Pacific abyssal sites.

6.2.3 Beta diversity patterns

Beta diversity, or species turnover, can be measured using the random species accumulation method (section 3.3.4). The species accumulation curves for all the sites are plotted in Figure 6.12. It is apparent that none of the curves show any signs of reaching asymptote, indicating that none of the sites have been fully sampled. The rate of increase in species number with increasing area may be in this case either a function of beta diversity, or a function of abundance. The highest accumulation rate of species is observed at the EqPac phytodetrital sites, and the lowest at the north Atlantic MAP site. Species accumulation is higher at the EqPac phytodetrital sites than at the PAP site, which has very similar levels of abundance, indicating that beta diversity may be higher at EqPac than at PAP. Similarly, there are more species in a similar area of seabed at the DOMES A site than at the north Atlantic MAP site – again, both sites have very similar levels of abundance.

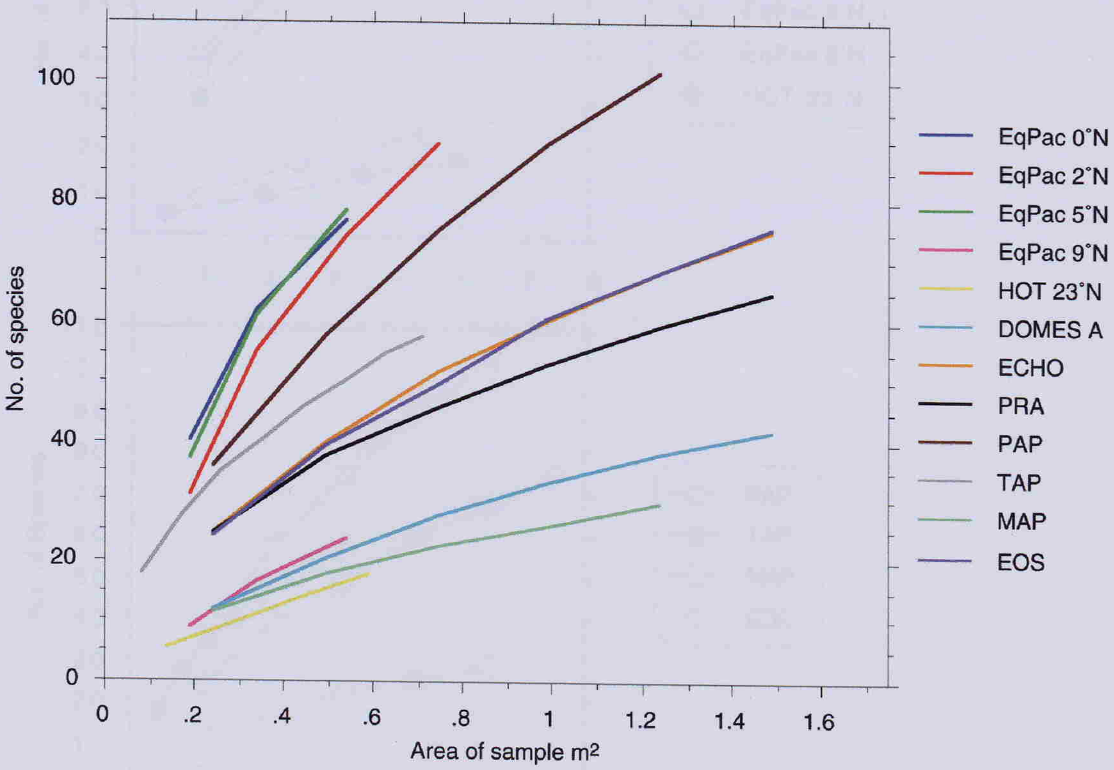


Figure 6.12 Beta diversity as measured using the species accumulation curve at all abyssal sites. Note that the analysis was halted at a sample size of 1.5 m^2 as only the DOMES, ECHO and PRA sites had larger sampling areas.

Species accumulation curves are split by sampling locality in Figure 6.13. At the EqPac sites, species accumulation is most rapid at the phytodetrital sites compared with the non-phytodetrital ones. At the north Atlantic sites, species accumulation was most rapid at the PAP site, then the TAP site, followed by EOS and finally MAP. 1 m^2 of seabed at PAP contained on average, 90 species, compared to 60 at EOS and 20 at MAP. At the manganese nodule sites, species accumulation was more rapid for the ECHO 1 and PRA sites, and reduced at the DOMES A site. The DOMES A site is the only abyssal sampling station where enough samples have been taken for the species accumulation curves to show any sign of reaching asymptote.

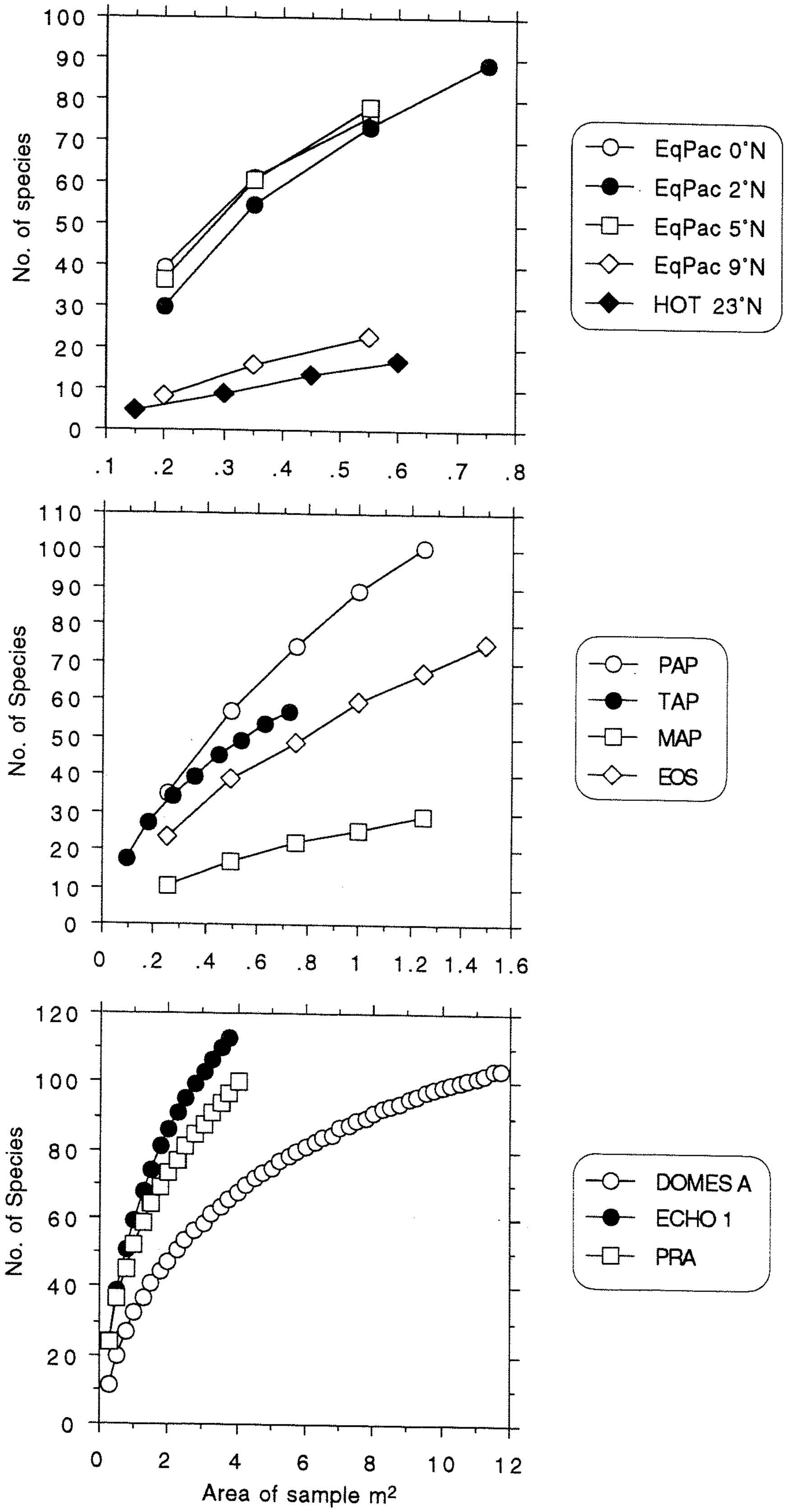


Figure 6.13 Species accumulation curves for individual regions.

An alternative way of examining beta diversity is to use multivariate techniques to generate a percentage similarity figure between sites. At a species level, this has been done for sites within the three sampling locations – the EqPac sites, the manganese nodule sites and the north Atlantic sites, as each dataset uses unique species identifiers. The Kulczynski similarity index results (Table 6.3) indicates that the intensity of sampling makes a significant impact on the degree of similarity between sites. The intensely sampled manganese nodule sites show the highest similarity levels (49-64%), followed by the EqPac phytodetrital sites (46-51%) and the north Atlantic sites (20-26% similarity). The distance between sampling sites is indicated in subscript next to the percentage similarity, and these values are plotted in Figure 6.14.

At the EqPac sites, there is no clear relationship between Kulczynski percent similarity and distance at the scale of a few hundred km. Percent similarity varied from 46% between 2°N and 5°N to 51% between 0°N and 5°N.

At the manganese nodule sites, there was a slight trend towards increased similarity with reduced distance; the closest sites physically – PRA and ECHO 1, separated by just 280 km – also showed the highest percentage similarity, 64%.

At the north Atlantic sites, similarity was universally low, with sites sharing only 20-26% of species; there was no clear relationship with distance. The most distant sites, PAP and EOS (3356 km) had a similarity level of 21%, the closest, PAP and TAP (1183 km) had a slightly higher similarity level of 26%.

	EqPac 0°N	**EqPac 2°N**	**EqPac 5°N**
EqPac 0°N	*	*	*
EqPac 2°N	$_{\text{222km}}$ 50%	*	*
EqPac 5°N	$_{\text{556km}}$ 51%	$_{\text{333km}}$ 46%	*

	DOMESA	**PRA**	**ECHO1**
DOMES A	*	*	*
PRA	$_{\text{2502km}}$ 55%	*	*
ECHO 1	$_{\text{2739km}}$ 49%	$_{\text{280km}}$ 64%	*

	MAP	**PAP**	**EOS**
MAP	*	*	*
PAP	$_{\text{1936km}}$ 20%	*	*
EOS	$_{\text{1518km}}$ 26%	$_{\text{3356 km}}$ 21%	*
TAP	$_{\text{1200km}}$ 21%	$_{\text{1183 km}}$ 26%	$_{\text{2711 km}}$ 20%

Table 6.3 % Kulczynski similarity for all abyssal sites; distance between sites in subscript.

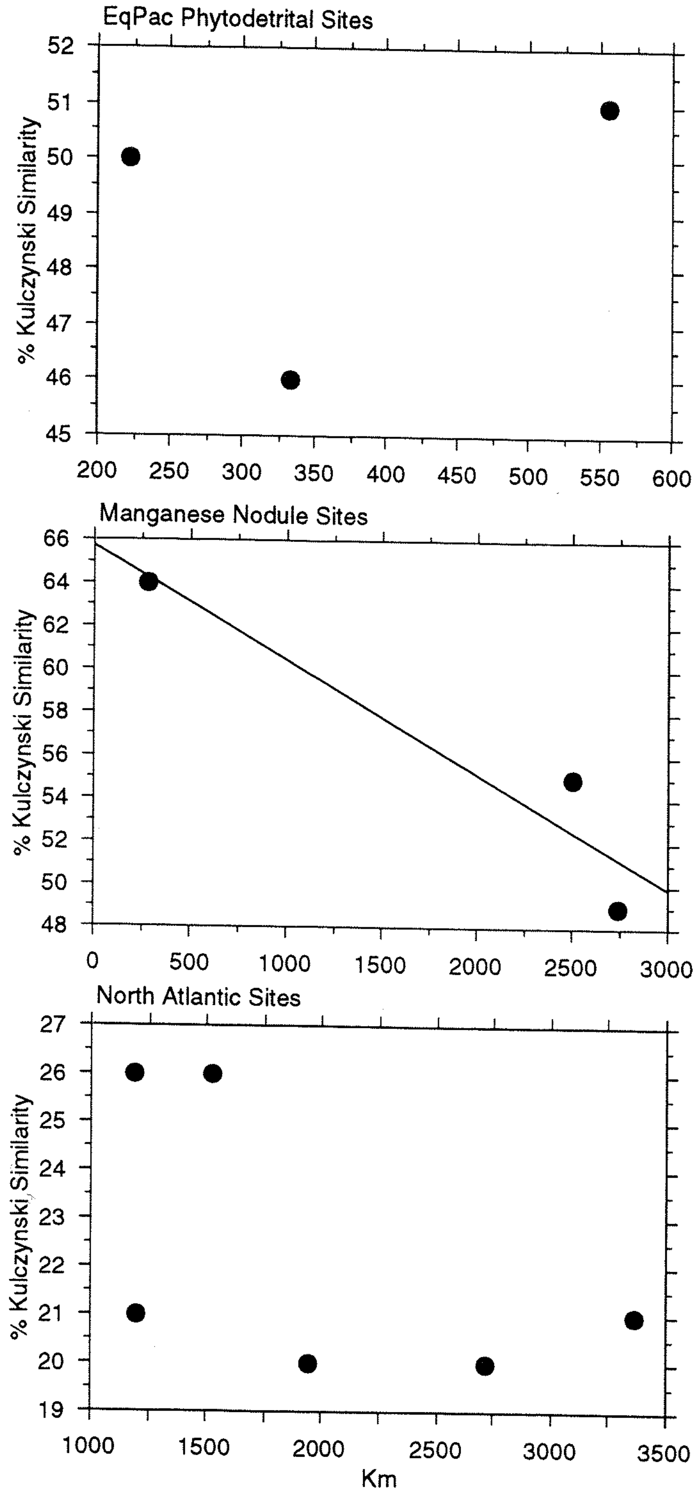


Figure 6.14 % Kulczynski similarity index plotted against distance between sites.

An alternative method to the Kulczynski index is the NESS measure, which accounts for sample-size using the same principle as the rarefaction method (section 3.3.6). Figure 6.15 indicates the NESS method applied to the EqPac data at two different sub-sample sizes, $m=1$ and $m=10$. At $m=1$, only the most dominant species are sampled and the index is equivalent to the Morista-Horn absence/presence index; at $m=10$, the influence of rare species is increased. The low abundance at the non-phytodetrital sites results in very low levels of similarity between box cores. There is no obvious grouping based on sites, with all of the EqPac phytodetrital sites clustering together. When a larger value of *m* is used, the phytodetrital region forms one cluster, but there is no apparent distinction between individual sites, reinforcing the notion that the phytodetrital region may represent a single faunistic province.

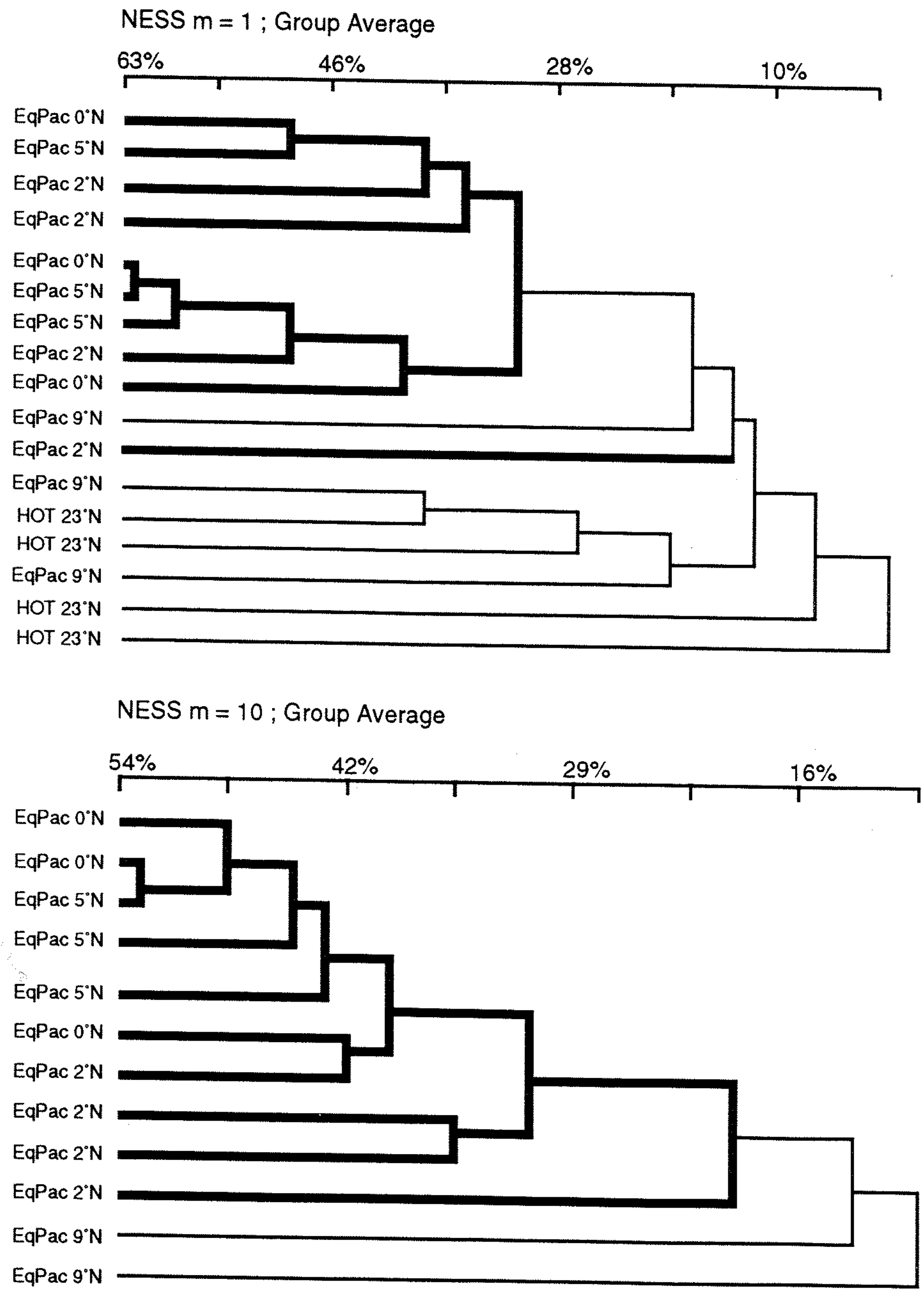


Figure 6.15 NESS similarity index for EqPac sites, clustered using group average method (UPGMA) at m=1 and m=10 sample sizes. Cores containing less than ten individuals not included in lower plot. Phytodetrital sites indicated by thickened lines.

For the manganese nodule provinces, clustering was performed at the m=5 and m=10 levels (Figures 6.16 and 6.17). Box cores within the ECHO 1 and PRA sites cluster into groups, but there are some exceptions. The DOMES A site, with the most box cores, appears to encompass the entire range of potential similarity levels: ECHO 1 and PRA form clusters within the overall DOMES A group. This indicates that the clustering of the ECHO 1 and PRA sites may in fact be an artifact of sample size, and that the entire equatorial Pacific region shows little variability in faunistic composition.

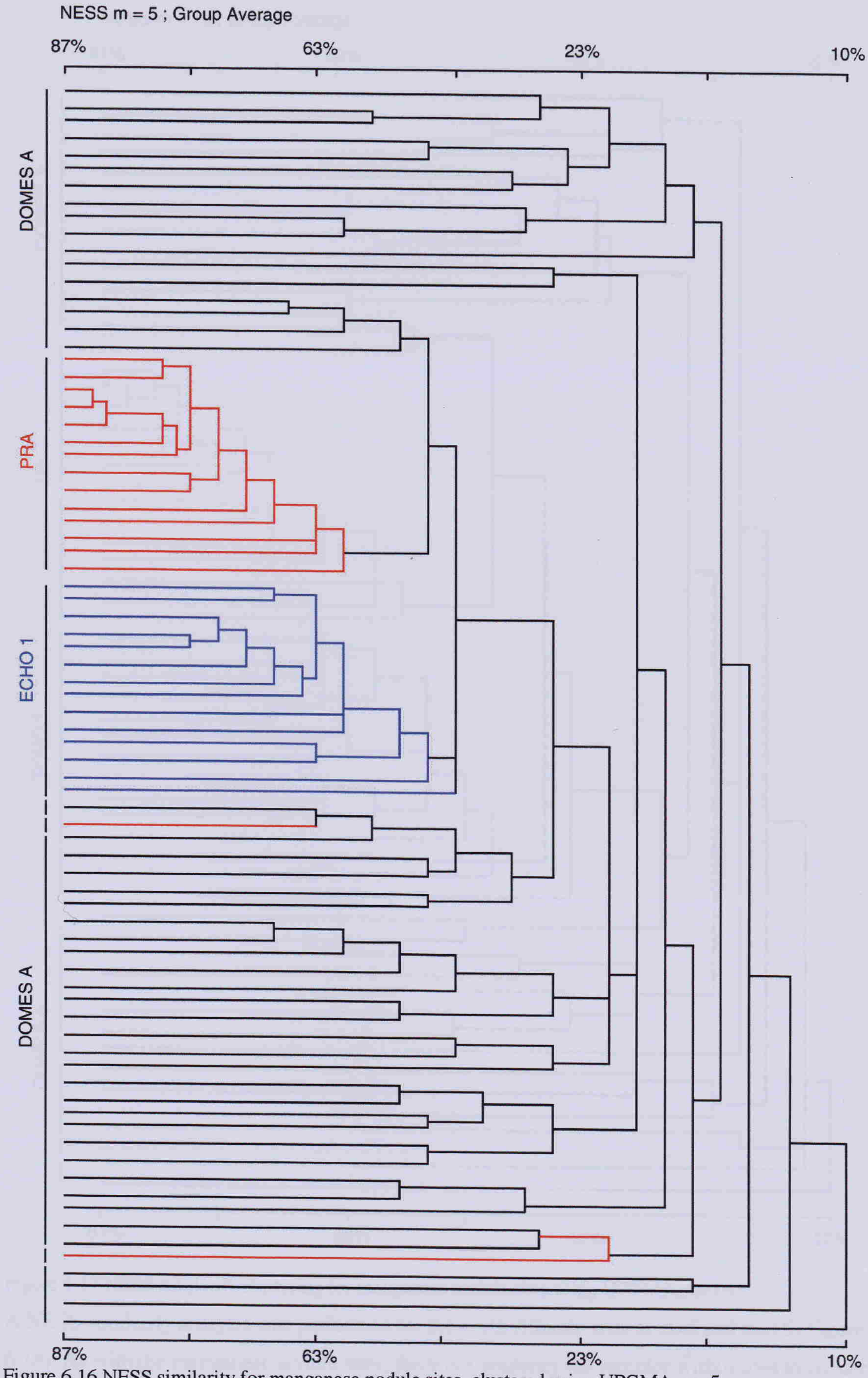


Figure 6.16 NESS similarity for manganese nodule sites, clustered using UPGMA, *m*=5.

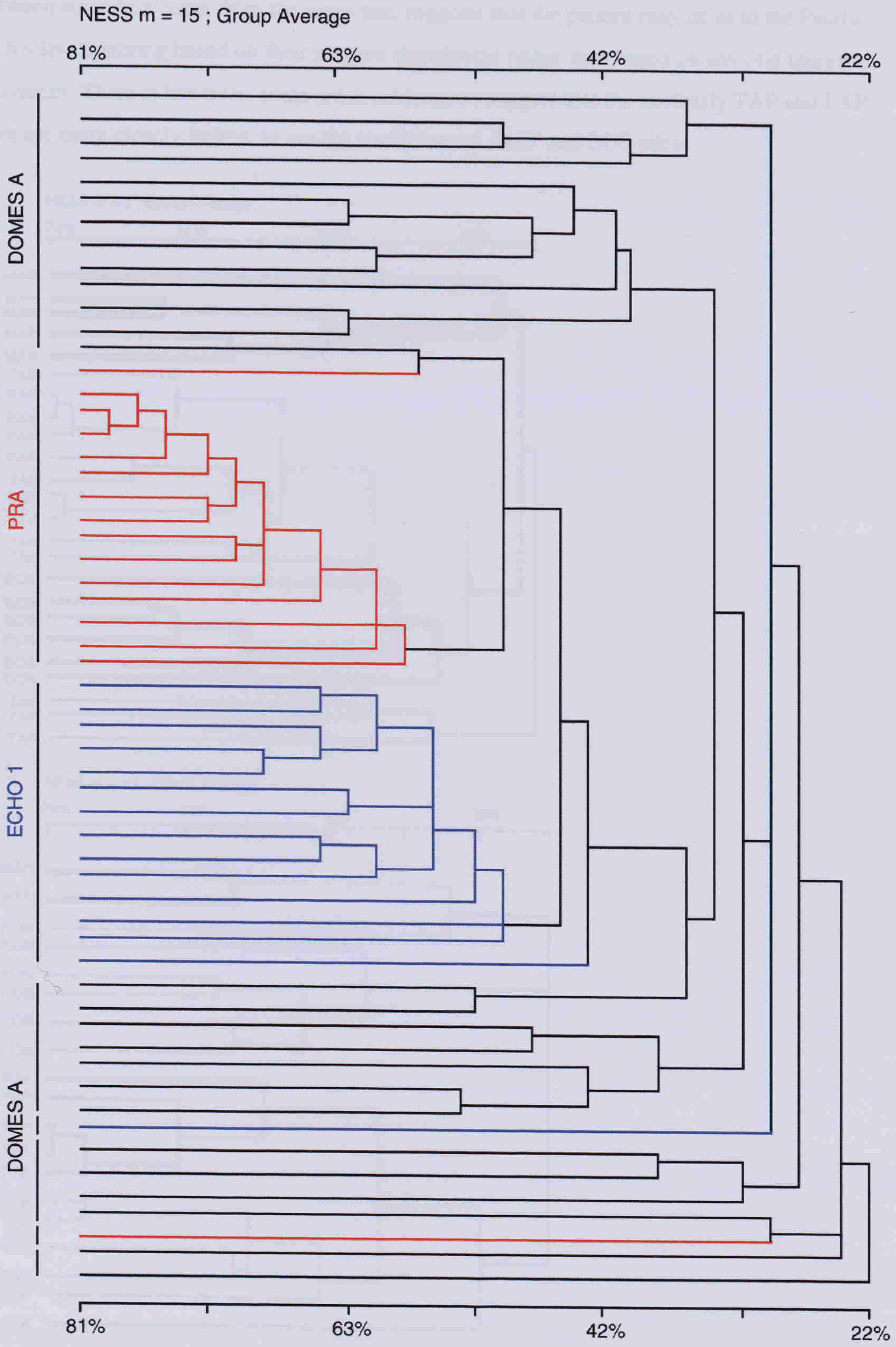


Figure 6.17 NESS similarity clustering for manganese nodule sites using UPGMA, *m*=15.

A NESS similarity analysis was performed for the north Atlantic sites at *m*=5 and *m*=15 (Figure 6.18). As with the manganese nodule sites, there is a tendency for samples within sites to cluster together. However, the pattern of clustering, and the very low levels of percent similarity seen between some box cores from the same site, suggests that the pattern may be as in the Pacific, with sites clustering based on their relative abundances rather than based on any real faunistic provinces. There is however, some weak evidence to suggest that the northerly TAP and PAP sites are more closely linked, as are the southernmost MAP and EOS sites.

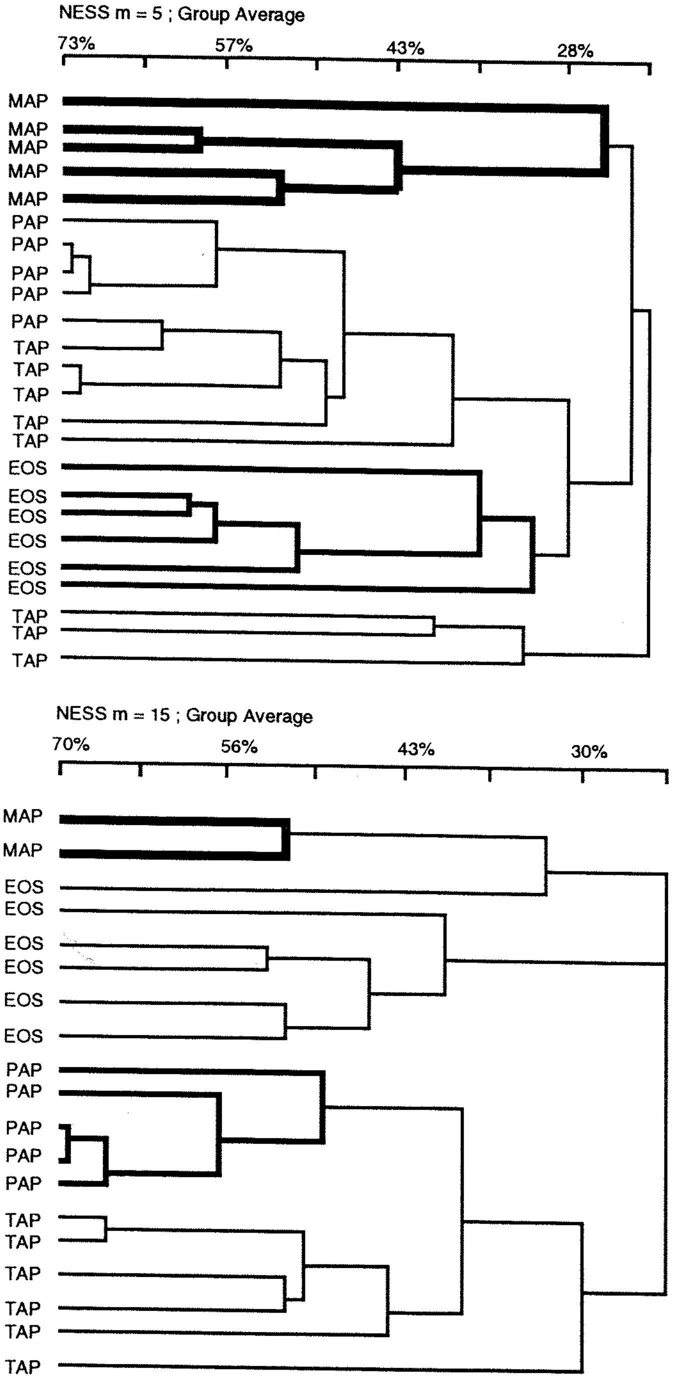


Figure 6.18 NESS similarity clustering for north Atlantic sites using UPGMA, m=5 and m=15. Discrete clusters indicated by thickened lines.

All of the analyses performed so far have been on unpooled individual box cores. Although more abundant sites show higher levels of similarity between box cores, there is still evidence that there may well be a high level of beta diversity, with sites only sharing 25-50% of species.

In this following section, this hypothesis is disproved, and the impact of sample-size on the previous analyses confirmed.

The NESS similarity analysis was repeated using pooled samples, in order to increase the number of individuals that can be used in the analysis. For the EqPac sites, the pattern was again of increasing levels of similarity in the more abundant phytodetrital sites (Figure 6.19). Although the phytodetrital sites form a discrete cluster, this does not provide convincing evidence of a 'phytodetrital' fauna, as the non-phytodetrital sites do not cluster together, and form a grade of reduction in similarity caused primarily by the absences of species. The two most closely related sites, EqPac 0°N and 5°N, had similarity levels approaching 70%, even though they were not the most close in terms of distance, separated by 556 km.

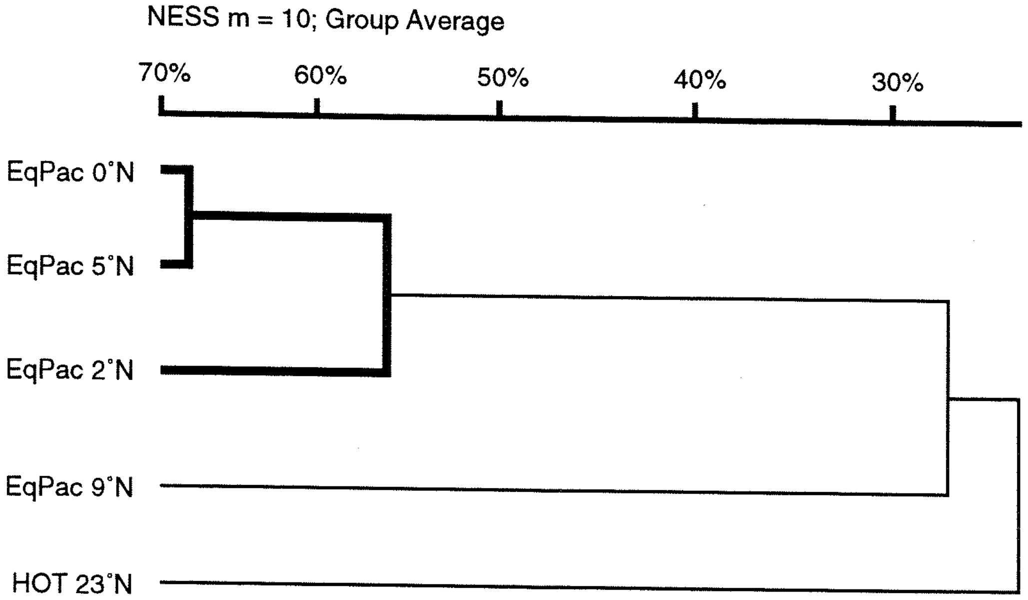
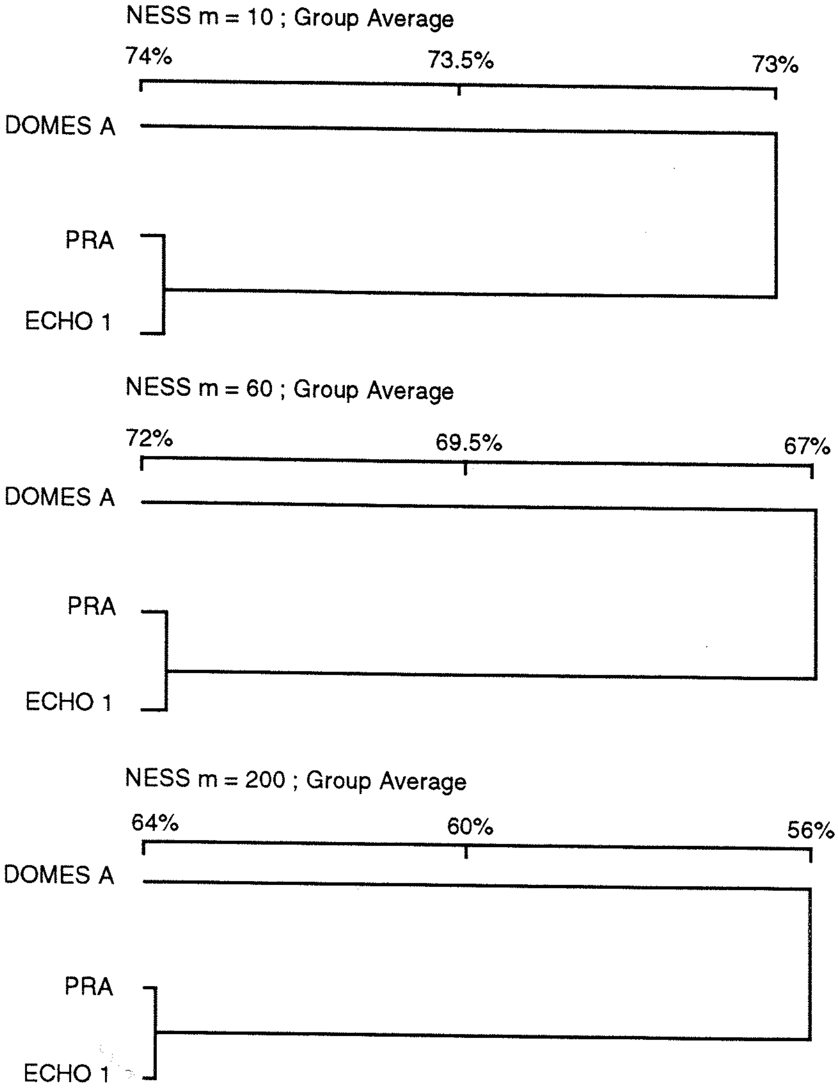


Figure 6.19 NESS similarity at *m*=5 for EqPac and HOT sites, clustered using UPGMA. Thickened lines indicate phytodetrital sites.

The same analysis performed on the manganese nodule dataset is indicated in Figure 6.20. At *m*=10, where only the dominant species are considered, there is very little difference in similarity between the three sites (all between 73-74%), although the physically proximal ECHO 1 and PRA sites cluster together. When *m* is increased to 60, the similarity levels decline, as more rare species are included in the analysis. The strength of the clustering of ECHO 1 and PRA also increases (5% difference between nodes, rather than 1%). At m=200, where many rare species are included in the analysis, the difference between nodes rises to 10%, and the sites overall are less similar.

A similar trend is observed for the north Atlantic sites (Figure 6.21). Overall levels of similarity are higher (66-43%) when more dominant species only are analysed (*m*=10); when *m* is increased to 50, similarity levels decline to between 52 and 33%. For both analyses, the more northerly PAP and TAP stations cluster together, indicating a potential distance effect, although there is no obvious split into the stations receiving phytodetritus, and those that do not.


NESS m = 10 ; Group Average

NESS m = 60 ; Group Average

NESS m = 200 ; Group Average

Figure 6.20 NESS similarity for three different values of *m* on the manganese nodule sites, clustered using UPGMA.

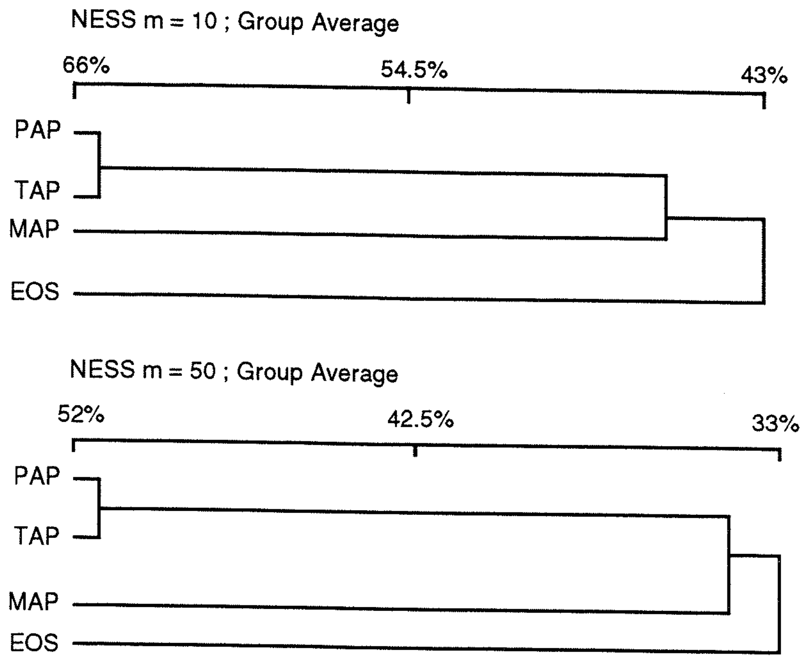


Figure 6.21 NESS similarity for north Atlantic sites, clustered using UPGMA.

The complete similarity matrix for Figures 6.19, 6.20 and 6.21 is given in Table 6.4, for the purpose of investigating the effect of distance on faunistic similarity. As was the case for the Kulczynski analysis, these values are plotted in Figure 6.22.

	EqPac 0°N	EqPac 2°N	EqPac 5°N	EqPac 9°N
EqPac 2°N	222km 57%	-	-	-
EqPac 5°N	556km 69%	333km 59%	-	-
EqPac 9°N	1000km 27%	778km 21%	444km 36%	-
HOT 23°N	3212km 23%	3034km 20%	2780km 24%	2468km 28%

	DOMES A	PRA		
PRA	2502km 74%	-	-	-
ECHO 1	2739km 73%	280km 74%	-	-

	PAP	TAP	MAP	
TAP	1183km 67%	-	-	-
MAP	1936km 39%	1200km 54%	-	-
EOS	3356km 53%	2711km 39%	1518km 37%	-

Table 6.4 NESS similarity matrix at *m*=10 for all abyssal sites. Distance between sites in subscript

There is no relationship between NESS similarity and distance at the north Atlantic or manganese nodule sites (Figure 6.22). At the EqPac sites, there is a slight trend towards increased similarity at the physically closer sites. However, NESS similarity is actually better explained by the abundance of the samples for the EqPac sites (Figure 6.22, lower graph). There is also a slight relationship between NESS similarity and abundance for the north Atlantic sites, although this is not the case at the manganese nodule sites, which do not vary in terms of abundance. This result suggests that NESS may be influenced by sample-size.

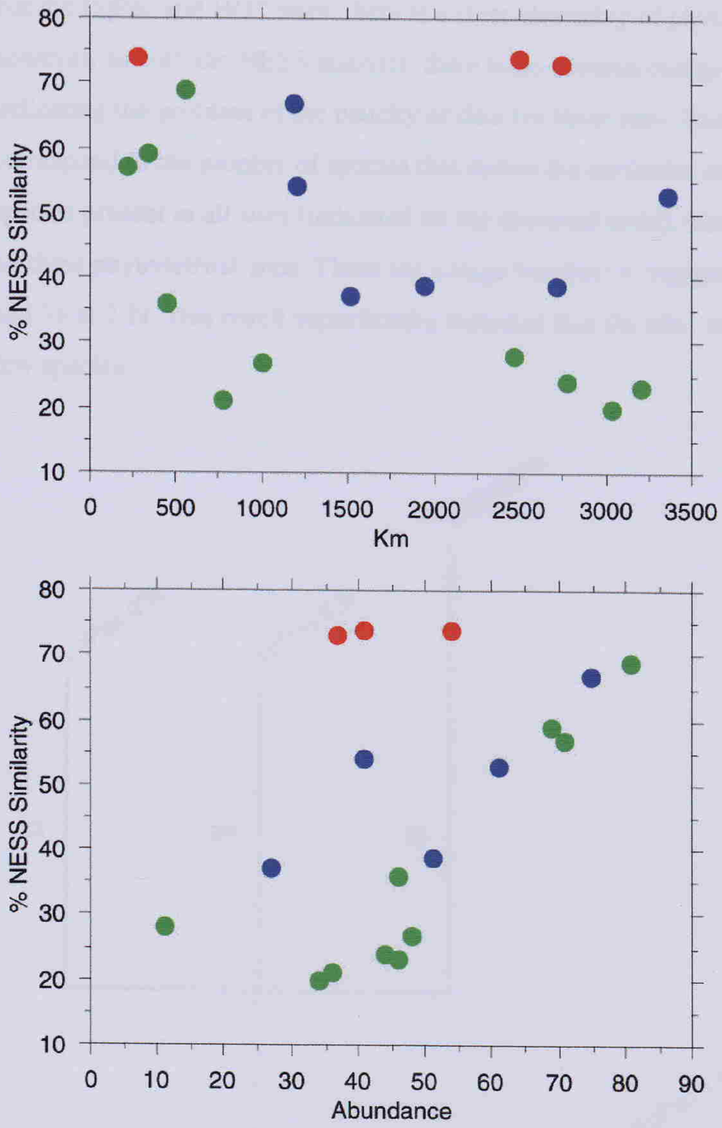


Figure 6.22 NESS similarity at m=10, plotted against distance between sites (top graph) and abundance (lower graph). Abundance has been calculated using a simple mean of the two sites being investigated.

6.2.4 Taxonomic composition

This section, although closely related to the previous, is intended to highlight variability in taxonomic composition between sites, rather than simply a percentage similarity at species level. Beta diversity is effectively a function of variability in taxonomic composition between 'putative' habitats such as the sites in this study.

The ecocladistic method has been used in the following figures 6.23, 6.24 and 6.25. This method uses a simple absence-presence dataset to group sites based on most parsimonious arrangements (see section 3.3.8). Although quantitative information is lost, this makes the measurement more sample-size independent, and it is useful in analysing simple changes in species composition rather than finer-resolution changes in species-abundance pattern that the NESS method analyses.

For the EqPac and HOT sites, there is a clear clustering of phytodetrital sites (Figure 6.23), however, as with the NESS analysis, there is no obvious clustering of non-phytodetrital sites, indicating the problem of the paucity of data for these sites. Branch lengths on the dendrogram correspond to the number of species that define the particular node. At EqPac, there are only 2 species present in all sites (indicated on the ancestral node), but there are 21 species present in all three phytodetrital sites. There are a large number of 'unique' species, 23 at 0°N, 23 at 5°N and 36 at 2°N. This result superficially indicates that the sites are highly derived, and share very few species.

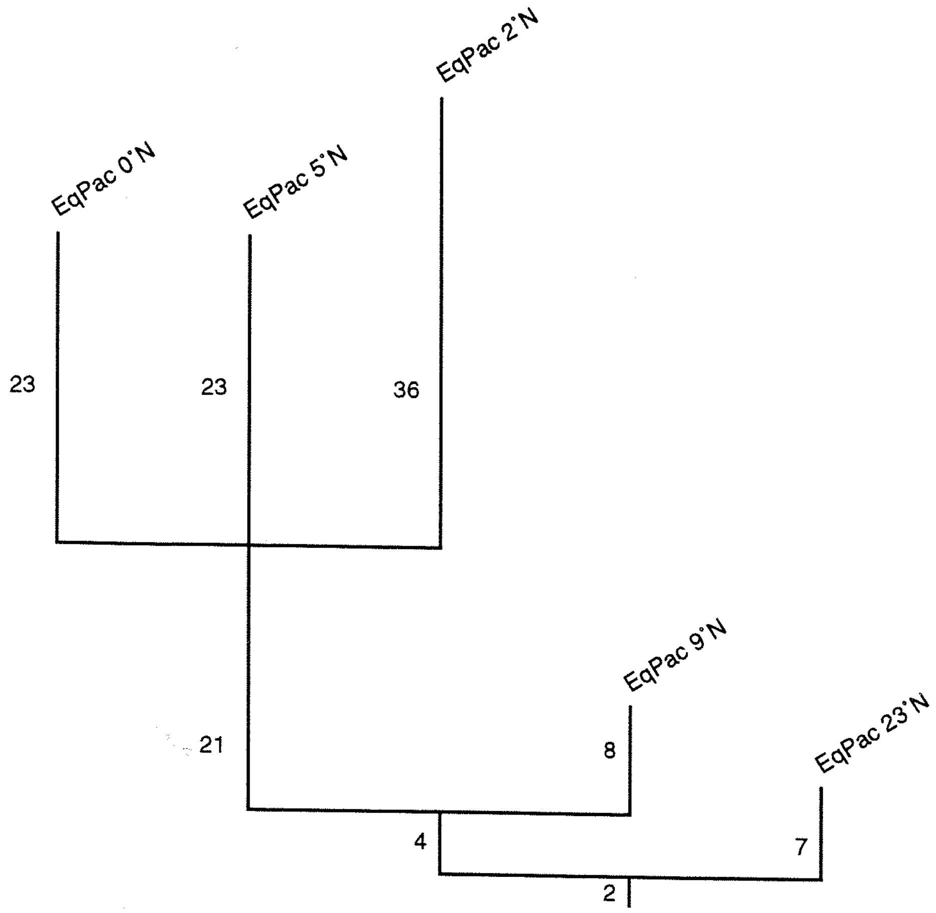


Figure 6.23 Cladogram of EqPac and HOT sites based on shared presences of species, analysed using PAUP 3.1. Branch lengths correspond to number of species that define each node. Strict consensus of two most parsimonious trees.

For the manganese nodule sites, the situation is slightly different, with many more cosmopolitan and widespread species (Figure 6.24). 43 species are present at all sites, and 25 at both ECHO 1 and PRA, the two sites which group together according to the most parsimonious arrangement. As at EqPac, a large number of unique species are also present, indicated by the long branch lengths of the terminal nodes.

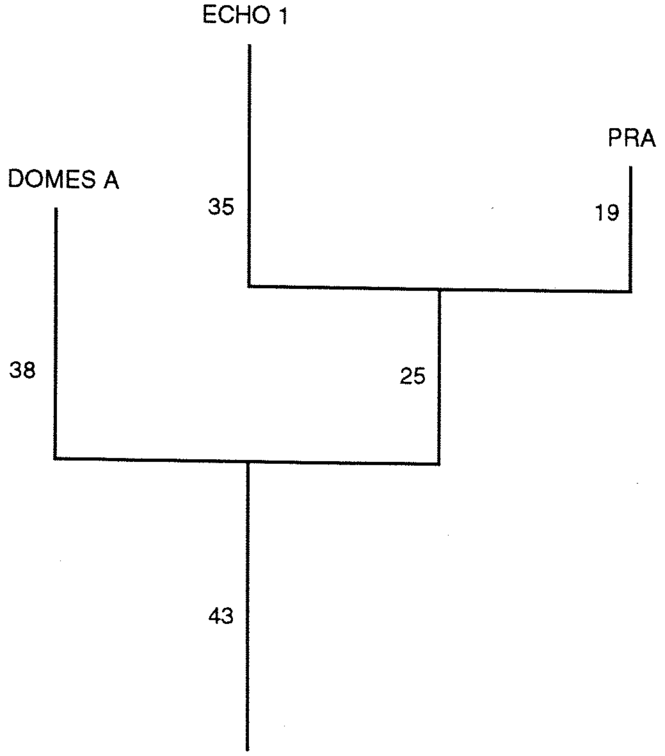


Figure 6.24 Cladogram of manganese nodule sites, analysed using PAUP 3.1. Branch lengths correspond to number of species that define each node. Single most parsimonious tree.

For the north Atlantic data (Figure 6.25), the great majority of species are uniques, only 5 species are cosmopolitan across all sites, and only 10 define the strongest clade, that of PAP and TAP. 67 species are unique to PAP, 33 to TAP, 20 to MAP and 52 to EOS.

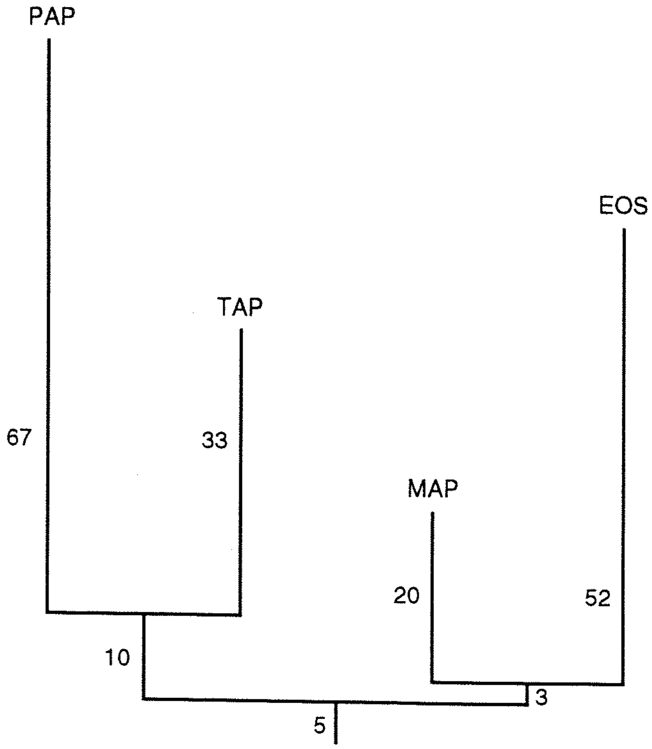


Figure 6.25 PAUP cladogram of north Atlantic abyssal sites. Single most parsimonious tree.

In order to illustrate graphically the importance of the long tail of endemic species, the north Atlantic sites have been used as an example of this in Figure 6.26. The entire species list is plotted graphically over the PAUP cladogram. Species diversity is enhanced by the presence of this large number of unique species, while the cosmopolitan species form a very small percentage of the species pool.

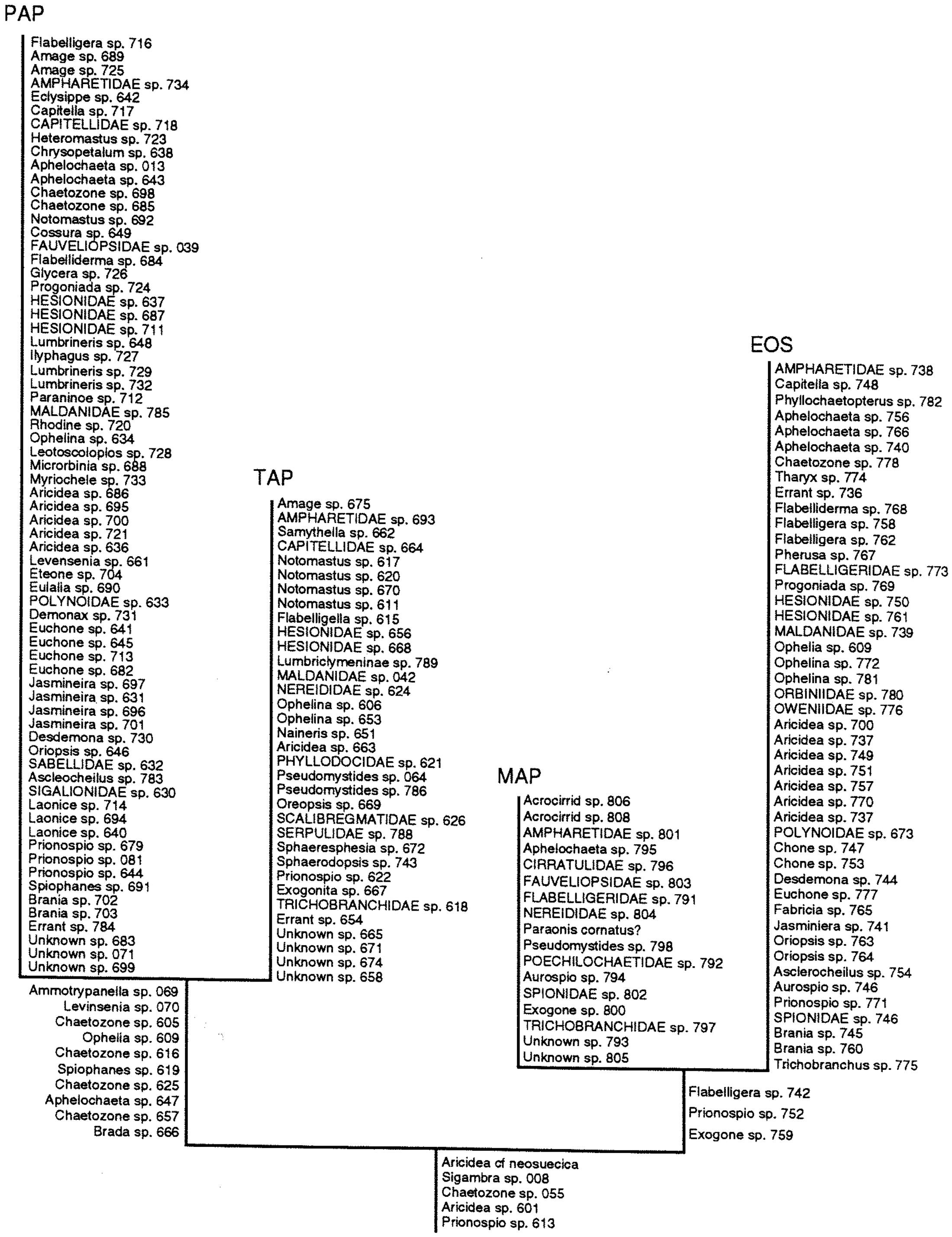


Figure 6.26 Cladogram derived from a single most parsimonious grouping of north Atlantic abyssal sites, with the entire species list plotted on to the PAUP parsimony output.

The question that asserts itself on observing the pattern in Figure 6.26 is – what is the proportion of individuals that each type of species represents? In other words, are, for example, the cosmopolitan species particularly abundant? This is explored further in the following graphs (Figures 6.27, 6.28 and 6.29). At the EqPac 0-5°N sites (the other sites were omitted for lack of data), the percentage of individuals that are cosmopolitan species is high, with 50-60% of the fauna being represented by the 21 cosmopolitan species (Figure 6.27). So although the greatest diversity lies in the unique species, the most common species are those that are cosmopolitan across all sites. This simple analysis indicates that these sites, even though they are separated by several hundred km are highly similar. Apart from the cosmopolitan species, three other types of species can be identified. 'Widespread' species are those that are present in two sites separated physically by at least one site (e.g. 0°N and 5°N). It is highly probable that a large proportion of these widespreads may in fact be cosmopolitan species which were missed at some of the sites. Regional species are those that are present in two sites that are not separated by a third site (e.g. 0°N and 2°N). At the EqPac sites, only 20-30% of the fauna (in terms of the number of individuals) are species that are found only at a single site (uniques).

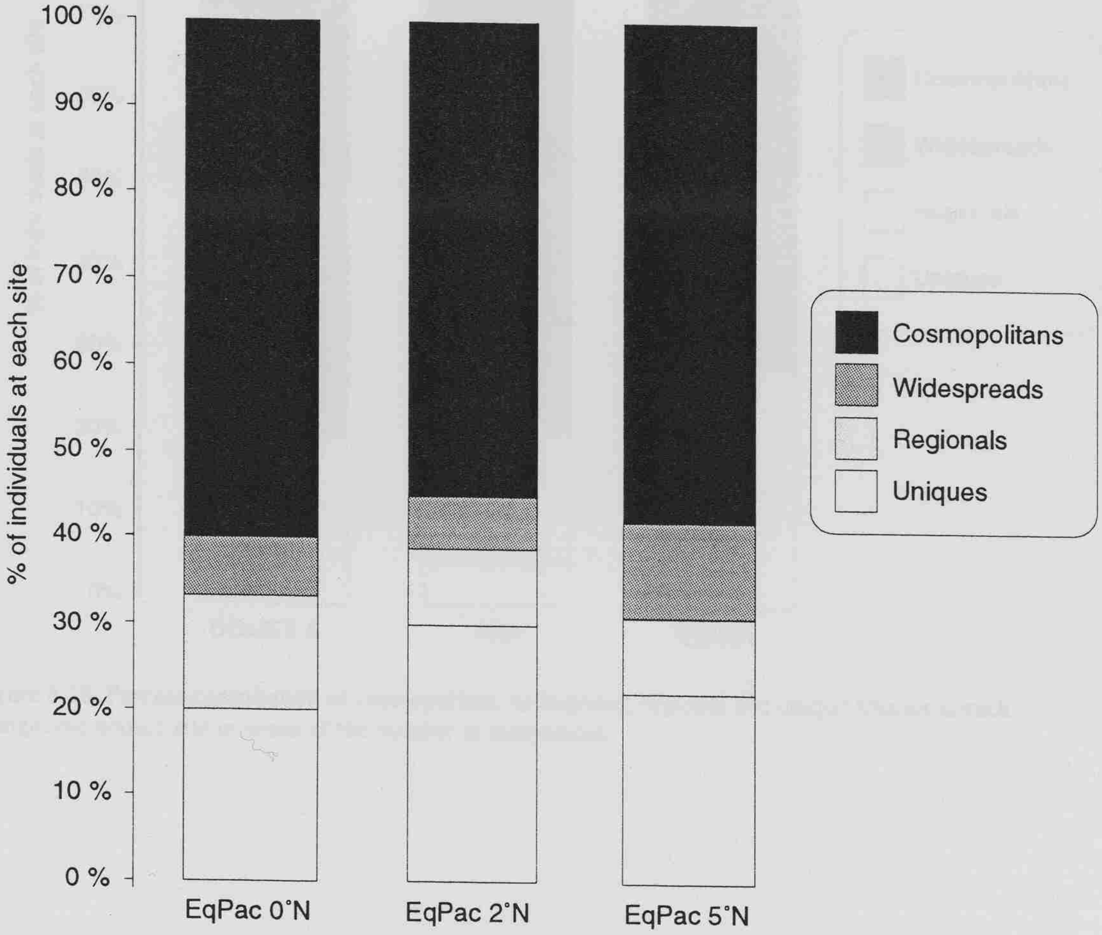


Figure 6.27 Percent contribution in terms of individuals of cosmopolitan, widespread, regional and unique species at the EqPac 0°N, 2°N and 5°N sites.

At the manganese nodule sites a similar pattern is observed. The percent contribution of the 43 cosmopolitan species is even higher, with 70-80% of the fauna, at all three sites, being composed of cosmopolitan species (Figure 6.28).

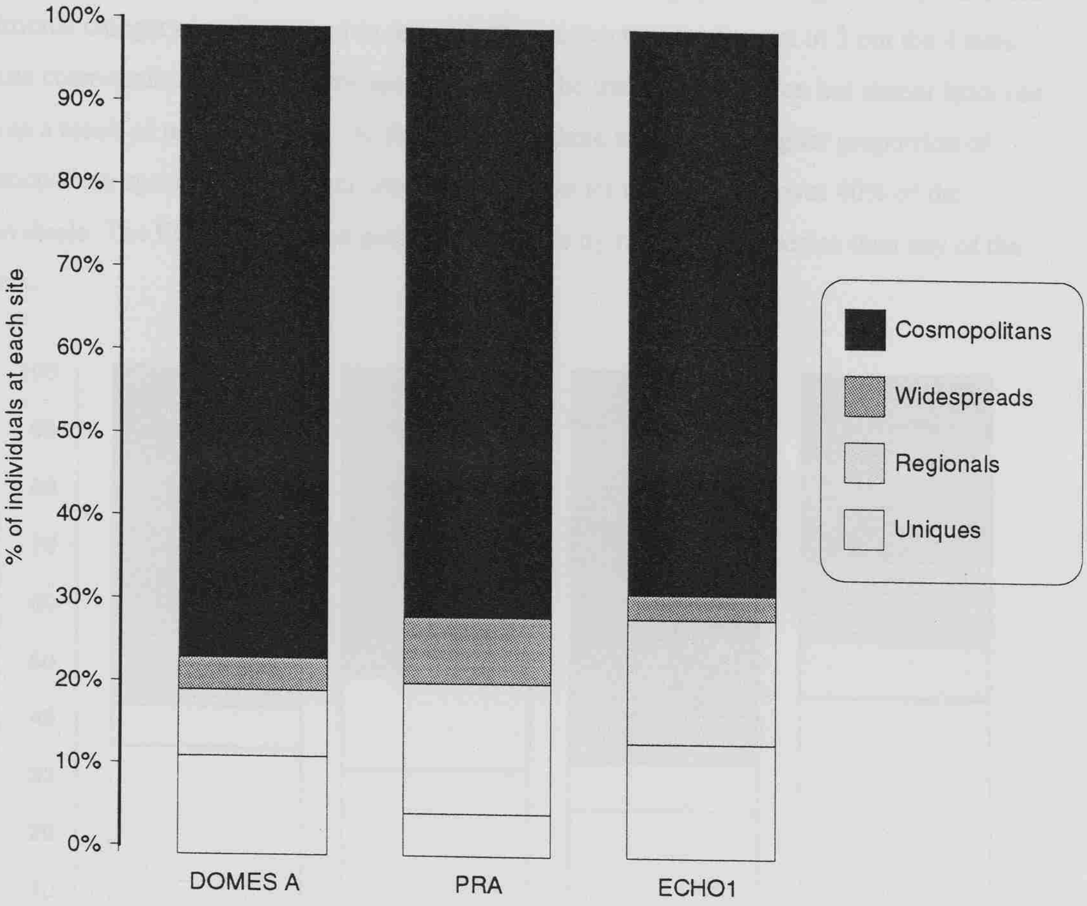


Figure 6.28 Percent contribution of cosmopolitan, widespread, regional and unique species at each manganese nodule site in terms of the number of individuals.

The same analysis has been carried out for the north Atlantic sites in Figure 6.29. In comparison with the manganese nodule sites, the proportion of individuals that are cosmopolitans is much smaller, although considering that there were only 5 recorded cosmopolitan species in the north Atlantic, the proportion of cosmopolitan individuals is still higher than might be expected. An additional category has been used in this case for species that are present in 3 out the 4 sites – '3-site cosmopolitans' – which are species likely to be truly cosmopolitan but absent from one site as a result of undersampling. At the MAP site, there was a much higher proportion of cosmopolitan species than at other sites. Just five species contribute to over 40% of the individuals. The EOS site showed greater dominance by rare, unique species than any of the others.

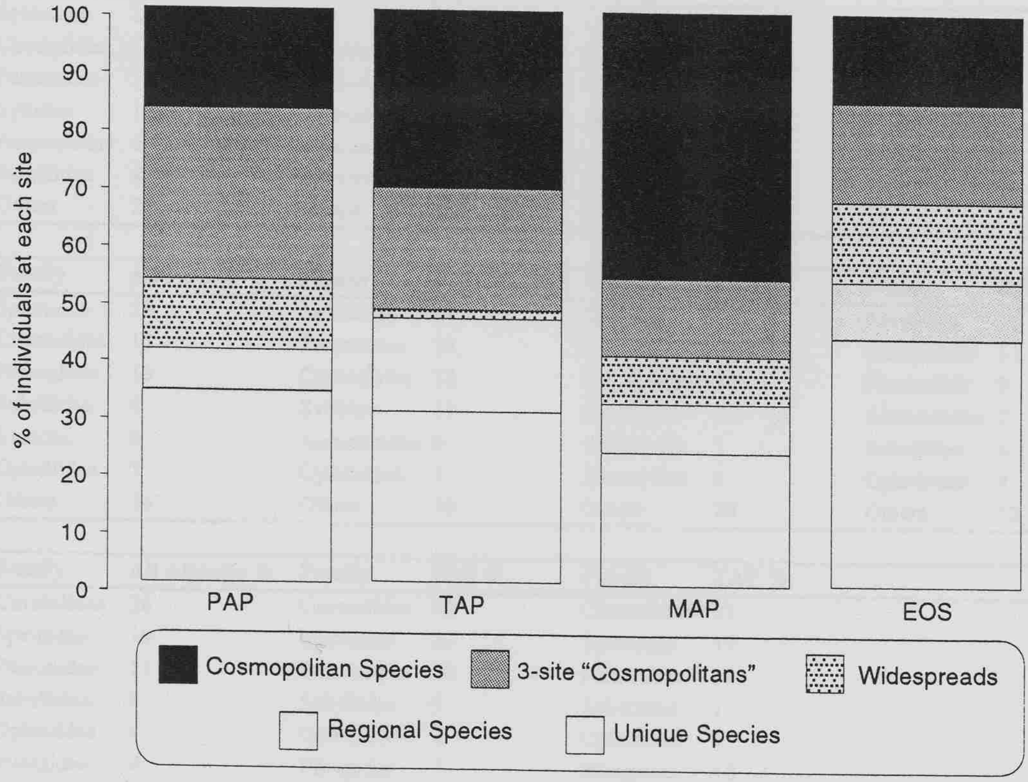


Figure 6.29 Percent contribution of cosmopolitan, 3-site cosmopolitan, widespread, regional and unique species at the north Atlantic abyssal sites.

The taxonomic composition at a family level is explored in the following section. At the EqPac sites, 31 families were identified; at the manganese nodules sites, 42, and at the north Atlantic sites, 32 families. The percentage contribution of the top six dominant families for each site is given in Table 6.5. 60-80% of the fauna is represented by the top six dominant families. This pattern was the same irrespective of the degree of sampling effort – at the well-sampled DOMES A site, 67% of the fauna is represented by six families, indicating that increased sampling effort does not significantly increase the relative abundance of the less dominant families. At every site, excluding the under-sampled EqPac 9°N and HOT 23°N sites, the cirratulids, paraonids and spionids are the three most abundant families, consistently representing approximately 50-55% of the fauna. There is some regional variation in the familial composition of the other dominant families. At EqPac, the syllids and acrocirrids are highly abundant, as they are at the nearby DOMES A site. In the north Atlantic, syllids and acrocirrids are less abundant, and they appear to be replaced by the opheliids and pilargids.

Family	All EqPac %	Family	EqPac 0°N %	Family	EqPac 2°N %
Spionidae	19	Spionidae	18	Cirratulidae	20
Cirratulidae	17	Cirratulidae	18	Paraonidae	15
Paraonidae	13	Paraonidae	12	Spionidae	14
Syllidae	13	Syllidae	11	Syllidae	11
Acrocirridae	7	Sabellidae	11	Acrocirridae	8
Sabellidae	6	Acrocirridae	6	Sabellidae	3
Others	25	Others	24	Others	29

Family	EqPac 5°N %	Family	EqPac 9°N %	Family	HOT 23°N %
Spionidae	25	Spionidae	17	Syllidae	30
Cirratulidae	14	Cirratulidae	14	Paraonidae	19
Paraonidae	13	Syllidae	13	Acrocirridae	15
Syllidae	13	Paraonidae	10	Spionidae	12
Acrocirridae	6	Acrocirridae	3	Cirratulidae	4
Sabellidae	4	Sabellidae	3	Sabellidae	0
Others	25	Others	40	Others	20

Family	All Nodule %	Family	DOMES A %	Family	PRA %	Family	ECHO %
Spionidae	23	Spionidae	19	Spionidae	19	Spionidae	31
Cirratulidae	13	Paraonidae	14	Paraonidae	15	Cirratulidae	11
Paraonidae	13	Cirratulidae	12	Cirratulidae	14	Paraonidae	9
Sabellidae	6	Syllidae	11	Sabellidae	11	Acrocirridae	7
Syllidae	6	Acrocirridae	6	Opheliidae	7	Sabellidae	6
Opheliidae	5	Opheliidae	5	Hesionidae	6	Opheliidae	4
Others	34	Others	33	Others	28	Others	32

Family	All Atlantic %	Family	PAP %	Family	TAP %
Cirratulidae	28	Cirratulidae	32	Cirratulidae	21
Spionidae	19	Spionidae	23	Spionidae	17
Paraonidae	11	Paraonidae	10	Paraonidae	12
Sabellidae	8	Sabellidae	9	Sabellidae	1
Opheliidae	4	Opheliidae	2	Opheliidae	11
Pilargidae	4	Pilargidae	1	Pilargidae	12
Others	27	Others	23	Others	26

Family	MAP %	Family	EOS %
Cirratulidae	9	Cirratulidae	35
Spionidae	21	Spionidae	11
Paraonidae	16	Paraonidae	10
Sabellidae	5	Sabellidae	11
Opheliidae	1	Opheliidae	3
Pilargidae	2	Pilargidae	1
Others	48	Others	28

Table 6.5 Percent family composition at all sites for the top six dominant families at each site.

Table 6.6 lists the number of species in each family. At EqPac, the cirratulids are the most species-rich taxon (19 species), followed by the spionids (17 species), the sabellids (16 species) and the syllids (12 species). At the manganese nodule sites, there is a greater evenness of species distributions amongst families, with the spionids and phyllodocids the most species-rich

(13 species), followed by the syllids, the sabellids and the opheliids (all with 11 species). In the north Atlantic, four families dominate the species richness – the cirratulids with 23 species, the sabellids with 22, the paranoids with 20 and the spionids with 19 species.

	No. of species at EqPac	No. of species at NODULE	No. of species at Atlantic
Acrocirridae	10	8	2
Ampharetidae	3	5	10
Capitellidae	3	6	9
Chaetopteridae	0	2	1
Chrysopetalidae	4	1	2
Cirratulidae	19	9	23
Dorvilleidae	1	2	0
Euphrosinidae	0	3	0
Fauveliopsidae	2	1	3
Flabelligeridae	3	4	8
Glyceridae	2	1	2
Goniadidae	3	2	3
Hesionidae	2	5	7
Heterospionidae	0	1	0
Lacydoniidae	0	1	0
Lumbrineridae	2	9	6
Magalonidae	0	1	0
Maldanidae	2	7	5
Nephtyidae	1	1	0
Nereididae	6	2	3
Onuphidae	0	2	0
Opheliidae	3	11	7
Orbiniidae	3	2	4
Oweniidae	0	2	2
Paralacydonidae	1	0	0
Paraonidae	10	8	20
Phyllodocidae	5	13	7
Pilargidae	1	2	1
Poecilochaetidae	0	1	1
Polynoidae	3	4	2
Questidae	0	1	0
Sabellariidae	0	1	0
Sabellidae	16	11	22
Scalibregmatidae	1	9	3
Serpulidae	0	6	1
Sigalionidae	3	3	2
Sphaerodoridae	4	2	2
Spionidae	17	13	19
Syllidae	12	11	7
Terebellidae	0	1	0
Trichobranchidae	1	4	3

Table 6.6 No. of species in each family at each abyssal region.

The 42 polychaete families were assigned functional groups according to the system of Fauchald and Jumars (1979). All jawed, potentially carnivorous species have been assigned to the 'PRED' group, although it is not known whether these animals are likely to be actual predators, or scavenging species. The functional group categories are described in Table 6.7, and the relative abundance of these categories is indicated in Table 6.8 and Figure 6.31. The PRED group, the SMT group and the SDT group are dominant at all abyssal sites. There is no fundamental change in functional group composition at phytodetrital sites, and there is no change associated with physical disturbance at MAP. There is a slight increase in the relative abundance of predator-scavengers at the Pacific sites compared to the Atlantic sites.

PRED	Predator-Scavengers (e.g. Syllidae)
SDT	Surface deposit feeder, discretely motile, tentaculate feeding structure (e.g. Spionidae)
SMT	Surface deposit feeder, motile, tentaculate feeding structure (e.g. Acrocirridae)
SMX	Surface deposit feeder, motile, other feeding structures (e.g. Paraonidae)
BSMT	Burrowing, or possibly surface, deposit feeder, motile, tentaculate (e.g. Flabelligeridae)
BMX	Burrowing deposit feeder, motile, tentaculate (e.g. Capitellidae, Sphaerodoridae)
SST	Surface deposit feeder, sessile, tentaculate feeding structure (e.g. Ampharetidae)
BSX	Burrowing, sessile, other feeding structures (e.g. Maldanidae)
FST	Filter-feeding, sessile, tentaculate (e.g. Sabellariidae)

Table 6.7 Description of feeding groups. Adapted from Fauchald and Jumars (1979).

	EqPac 0°N %	**EqPac 2°N %**	**EqPac 5°N %**	**EqPac 9°N %**	**HOT 23°N %**
PRED	29	31	26	41	46
SDT	29	17	30	21	12
SMT	18	20	14	14	4
SMX	12	15	13	10	19
BSMT	7	8	6	7	15
BMX	3	4	9	7	4
SST	2	1	1	0	0
BSX	0	3	0	0	0
FST	0	0	0	0	0

	DOMES A %	**PRA %**	**ECHO 1 %**
PRED	29	19	20
SDT	22	33	39
SMT	12	15	11
SMX	14	15	9
BSMT	6	3	7
BMX	10	12	9
SST	5	2	4
BSX	0	0	1
FST	3	0	1

	PAP	**TAP**	**MAP**	**EOS**
PRED	14	24	22	15
SDT	34	16	26	24
SMT	27	18	18	32
SMX	12	13	17	11
BSMT	2	2	4	9
BMX	7	20	3	7
SST	3	4	9	2
BSX	0	2	0	0
FST	0	1	0	0

Table 6.8 Relative abundance of functional groups.

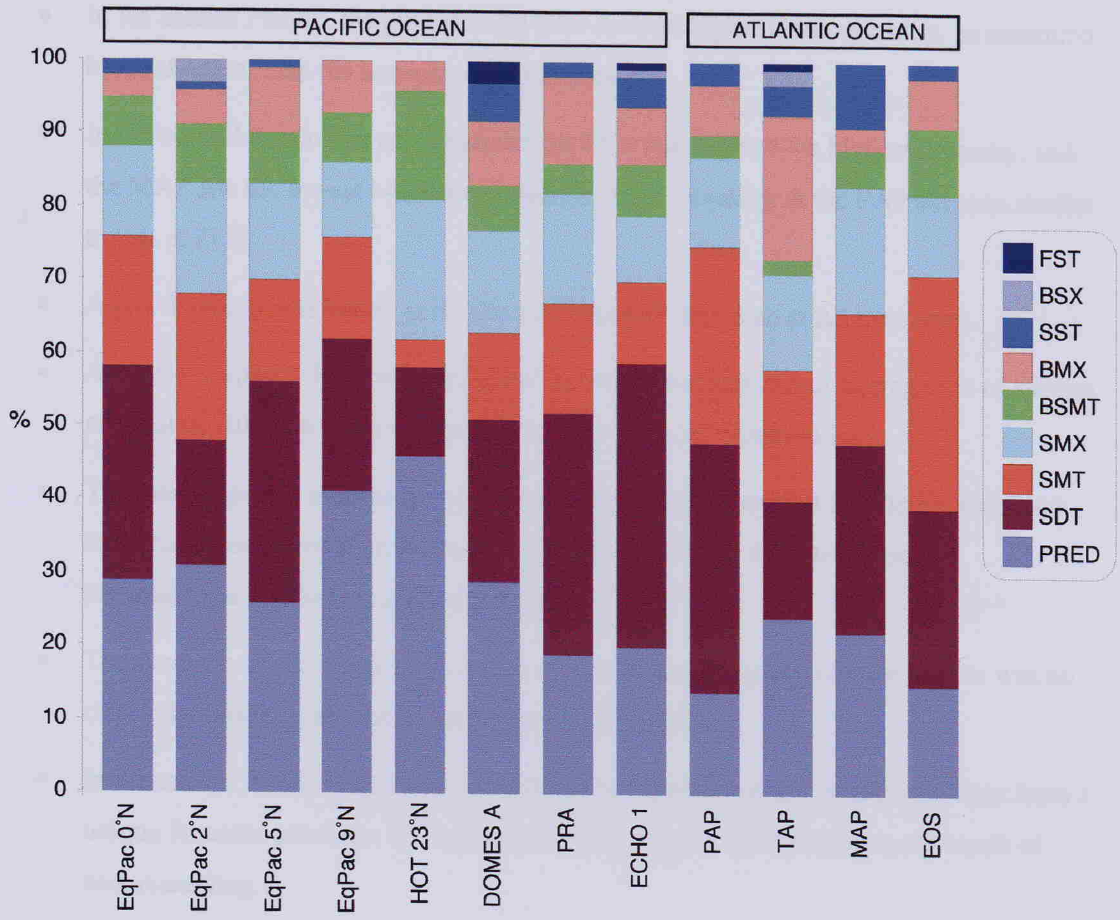


Figure 6.30 Percent of individuals belonging to functional groups at all abyssal sites.

6.3 Summary of Results

- In the central Pacific, the most food-rich sites, and the sites receiving a spatio-temporally patchy input of food (phytodetritus), showed the highest alpha diversity when measured using the Shannon H' diversity index, which is sensitive to species richness. H' was positively correlated with POC flux.
- In the north Atlantic, the phytodetrital PAP site showed similar levels of alpha diversity to the non-phytodetrital EOS site, although it was higher than at the TAP or MAP sites.
- There was little or no variation in the Simpson D index, which is more sensitive to equitability than Shannon H'.
- Shannon H' was shown to be sample-size sensitive in samples with less than 35 individuals. When the analysis was restricted to samples with more than 35 individuals, the phytodetrital sites still showed higher alpha diversity than the non-phytodetrital sites, although this was only significant for the Pacific sites.
- The rarefaction method of measuring species diversity was shown to be independent of sample size.

- In the central Pacific, the phytodetrital sites showed higher alpha diversity, as measured by rarefaction, than the non-phytodetrital sites.
- In the north Atlantic, the non-phytodetrital EOS site showed the highest diversity, and the MAP site the lowest - 40% lower than at EOS. Diversity at the PAP site was similar to that at EOS.
- Alpha diversity was higher at Pacific phytodetrital sites than at Atlantic ones.
- Analysis of spatial dispersion indicated that there was significant aggregation of species at all sites, although there was no relationship with phytodetrital input.
- The rate of species accumulation with area was higher at central Pacific phytodetrital sites than at non-phytodetrital ones. In the north Atlantic, the rate of species accumulation was lowest at the MAP site.
- The faunistic similarity of sites was closely related to sampling intensity, there was no clear relationship with distance at scales of 200-3000 km.
- In the central Pacific, there was no evidence to suggest that any of the sites were from a unique faunistic province, all sites were closely related and differences the result of undersampling.
- In the north Atlantic, percentage similarity over similar scales was lower, although the low similarity levels appeared to be the result of undersampling rather than any real changes in community composition.
- At both central Pacific and north Atlantic sites, a large proportion of the fauna, in terms of individuals, are cosmopolitan species that are widespread on scales of 2000-3000 km. Diversity is enhanced at individual locations by the presence of many rare or unique species.
- At a family level, all the sites are dominated by the top six families, which represent between 60 and 80% of the fauna. Cirratulids, spionids and paraonids represent 50-55% of the fauna at all sites.
- There was a difference in familial composition between Pacific and Atlantic sites, with acrocirrids and syllids more dominant in the Pacific, and opheliids and pilargids replacing them in the Atlantic.
- The most abundant families were also the most speciose, although there was a more even distribution of species in the more intensively sampled manganese nodule sites.
- There was little change in functional group composition between any of the sites, being unrelated to both oceanic province and phytodetrital input.

6.4 Discussion

Any scientific study must first establish a pattern, then suggest a process. In deep-sea ecology, establishing a pattern is a difficult task, and theory has been limited by such inconsistencies in observation. To evaluate hypotheses, or suggest new ones, patterns must be both consistent and reliable. With this in mind, this discussion follows the following format: firstly, small-scale patterns of alpha diversity are discussed, and the role of productivity, disturbance and regional enrichment in shaping them investigated. Secondly, the impact of large scale natural physical disturbance is examined. Finally, the patterns of beta diversity are examined and the implications for total biodiversity evaluated.

6.4.1 Small-scale patterns of diversity, and how to measure them

At a small spatial scale, polychaete diversity in the abyss is exceptionally high. At the EqPac sites, 155 species were discovered from just 3 m^2 of sediment. At the manganese nodule sites, 183 species were discovered from 20 m^2 of sediment. At the north Atlantic sites, 201 species were discovered from 4.75 m^2 of sediment.

Such attractively simple statements are, unfortunately, misleading. Firstly, as the samples within each region do not come from the same place: in the north Atlantic, the sites are separated by over 3000 km. The samples that make up the total of 4.75 m^2 may encompass more than one habitat, and hence be influenced by beta diversity. An analogy from terrestrial biology helps to indicate the problem: an ecologist investigating the diversity of grasslands could not take a single 1 m^2 sample in Europe, and a single 1 m^2 sample in North America and conclude that the diversity of 2 m^2 of grassland was the sum of the two. The greater the difference in species composition between European and North American grasslands, the greater the overestimation of diversity. Similarly, in the deep-sea, the greater the rate of species turnover between sites, the greater the exaggeration of diversity.

With this 'problem' of beta diversity in mind, a more valid comparison might be to count the number of species at a single site. At the EqPac 0°N site, 73 species were discovered from 0.54 m^2 of sediment. This could be compared to the HOT 23°N site, where just 14 species were discovered, from the larger area of 0.6 m^2. Does this mean that the HOT 23°N site is less diverse? Again, attractively simple measures of diversity such as this are actually meaningless in the abyssal situation. At EqPac 0°N, 175 individuals were sampled, compared to just 18 individuals at the HOT 23°N site. The undersampled HOT station is less diverse as less individuals have been collected, not because the community at 23°N is less diverse.

Simple measures of species richness cannot be used in undersampled deep-sea sites. Complex statistics, and probabilistic measurements of diversity must be employed for valid comparisons to be made. To measure alpha diversity in deep-sea sites, both the potential problems of species turnover and density-dependence must be accounted for. Recently, some authors have proposed using species accumulation curves with sampling area as a substitute for rarefaction (Gray, 2000). But such a method can only be used when sites have similar numbers of individuals per unit area. As was shown in Chapter 5, there is considerable variation in polychaete density in the abyss, and the use of diversity indices and rarefaction methods is the only way that such problems can be overcome.

6.4.2 The productivity-diversity relationship in the abyssal ecosystem

In an investigation of species diversity at 2100 m, Grassle and Maciolek (1992) concluded that:

> *"...high overall diversity appears to be maintained by the input of small patches of ephemeral resources and the disturbance that results from the activities of individual animals."*

In the central equatorial Pacific, the phytodetritus rich stations at 0°N, 2°N and 5°N showed the highest levels of diversity when measured using the Shannon diversity index and rarefaction methods, supporting the hypothesis of Grassle and Maciolek (1992). One of the problems in demonstrating this pattern conclusively was that the sample sizes at the EqPac 9°N and HOT 23°N stations were very low; however, when the data from the more intensively sampled manganese nodule sites was included, the pattern remained the same (Figure 6.9). The original hypothesis made in section 2.4 that an increase in productivity will generate an increase in diversity is supported by these data.

The EqPac phytodetrital sites do not differ only in the amount of food available. They also differ from the manganese nodule sites in terms of the spatio-temporal patchiness of food input, the presence of active bioturbating megafauna, increased microbial biomass, and a change in sediment composition, with a reduced $CaCO_3$ concentration at non-phytodetrital sites (Berelson *et al.*, 1994; Smith *et al.*, 1996; Stephens *et al.*, 1997).

Ecological theory suggests that all of these factors may play a part in increasing alpha diversity at the phytodetrital stations. Firstly, the near universality of the log-normal species abundance pattern (Preston, 1962) suggests that an increase in food resources will increase diversity (Rosenzweig, 1995). Rosenzweig proposes the following explanation for why this is so. Assume that two sites with differing levels of productivity start with the same diversity. Because overall abundance is higher in the more productive site, and diversity is the same, the rarest species in the more productive site must be more abundant – because of the log-normal distribution of species abundances. Hence in the more productive site, the scarce species will better resist accidental extinction. Diversity, therefore, must change until the rare species in all the sites have equal chances of accidental extinction, which means that '*... because the pie is larger in a more productive place, it must be sliced into many more pieces before its smallest are about the same size as the smallest in a poorer place*' (Rosenzweig, 1995).

According to Rosenzweig, much of the increase phase of the productivity-diversity hump may be explained by this process, although it is clear that accidental extinction is not the only process limiting diversity in the abyss. Furthermore, there have been many recent discussions regarding the 'universal' nature of the log-normal distribution and whether it is a sampling artifact or a real pattern (Lambshead *et al.*, 1983; Williamson, 1988). At very high levels of productivity, ecological theory suggests that diversity is limited by competitive exclusion, although a plethora of alternative theories have been implicated in this process (Rosenzweig and Abramsky, 1993). In the food-limited abyssal ecosystem, it appears that communities lie quite clearly on the increase phase of the unimodal curve, supporting the data of Cosson-Sarradin *et al.* (1998) in their analysis of polychaete diversity at food-rich sites near the west African upwelling.

At EqPac, not only is there a greater amount of food, but there is increased patchiness in food distribution, on both spatial and temporal scales. Smith *et al.* (1996) reported the presence of visible phytodetritus at the 0°N, 2°N and 5°N sites. Grassle and Morse-Porteous (1987), Grassle (1989) and Grassle and Maciolek (1992) have hypothesised that phytodetritus and associated patchiness of food, caused by collection in the depressions and burrows of benthic animals, should increase diversity at small spatial scales. The evidence from the EqPac transect supports this hypothesis. Between the EqPac phytodetrital sites, and the most species rich manganese nodule sites, there is a 30% reduction in species diversity, as measured by rarefaction.

Associated with enhanced productivity at the EqPac phytodetrital sites was the increased abundance of echinoderms, in particular large urchins, which were visible in seabed photographs (Smith *et al.*, 1997). The bioturbation generated by these organisms was ten-fold greater at the EqPac phytodetrital sites compared to the 9°N site (Smith *et al.*, 1997). Evidence from studies in shallow-water have shown how localised small-scale disturbance may increase diversity (Connell, 1978; Sousa, 1979; Kendall and Widdicombe, 1999; Widdicombe and Austen, 1999). Small-scale disturbance at EqPac may be responsible for the observed increases in diversity.

The EqPac phytodetrital sites also differed from the non-phytodetrital ones in their sediment characteristics. Etter and Grassle (1992), in a review of a large deep-sea dataset from the north-west Atlantic, concluded that sediment diversity was strongly correlated with species diversity. Amongst the sediments at 0-5°N were a high proportion of foraminiferal tests, with a $CaCO_3$ concentration of 80% (Berelson *et al.*, 1994). At 9°N, the sediments were composed of thick, 'soupy' clays, with numerous manganese nodules. Hence an alternative explanation for the high diversity at EqPac is a change in sediment characteristics, although it is likely that the observed differences in sediment characteristics are themselves the product of the different overlying productivity regimes.

In summary, the increased diversity at EqPac could be the result of increased productivity *per se*, spatio-temporal patchiness of food distribution, small-scale disturbance by bioturbators or finally, a change in sediment composition.

The reader will have observed by now that there has been no mention of the productivity-diversity pattern in the north Atlantic. We should take heed of Darwin's warning in the opening quote, and the more famous one by Thomas Henry Huxley:

> *"My business is teach my aspirations to conform themselves to fact, not to try to make facts harmonise with my aspirations."*

Given that the data from the Pacific ocean suggest that diversity is higher in areas receiving phytodetritus, one might expect diversity in the north Atlantic to be highest at the PAP site. But in fact, as Figure 6.10 shows, diversity at the supposedly oligotrophic EOS site is the same as at PAP.

In the north Atlantic, diversity is lowest at the MAP site, where it is about 30% lower than at PAP and EOS. The TAP site is slightly less diverse than the PAP site. In other words, were the EOS site to be removed from the analysis, then there would be a clear effect of productivity, as Lambshead *et al.* (1995) demonstrated in a comparison of PAP and MAP. But this would not exactly be following the advice of T.H. Huxley, to *'...give up every preconceived notion, follow humbly wherever nature leads...'*. A surprising and confounding observation is not the end of an investigation - it signals the start.

The lack of a clear relationship between food input and species diversity in the north Atlantic casts doubt, not on the pattern in the central Pacific, but on the cause of it. The observed pattern in the north Atlantic may actually shed light on the important variables that are influencing diversity in the Pacific sites. Rather than continuing to discuss the productivity-diversity question at this stage, the remainder of the important patterns are discussed in the following sections, and in the light of them, the productivity question is revisited in the final chapter.

6.4.3 The effects of physical disturbance in the north-east Atlantic

The MAP samples were characterised by lower species diversity and higher dominance than at the other north Atlantic sites (Figures 6.6, 6.8). Such dominance is unusual in deep-sea samples although sites such as the high energy HEBBLE site in the north-west Atlantic also have high sample dominance (Thistle *et al.*, 1985). At bathyal depths, high dominance was also noted by Paterson and Lambshead (1994) from areas swept by currents. The taxonomic composition at MAP is characterised by species with cosmopolitan or widespread distributions within the study sites in the North-east Atlantic abyss (Figure 6.29). These observations are reminiscent of a site undergoing recolonisation from disturbance. In shallow water, recovery from disturbance is categorised by lower diversity, high dominance and opportunistic species with wide distributions. It is difficult to identify an obvious disturbance agent. MAP is essentially quiescent with local currents speeds below 7 cms^{-1}. However, it will be recalled from Section 1.4 that the geological surveys of the MAP area in the mid 1980's indicated that the region had been affected by a relatively recent turbidite emplacement.

Rice *et al.* (1994) hinted that the MAP area may still be influenced by the effects of this turbidite. Given the age of the turbidite, which has been estimated at 1000 years, it might be expected that any effects would have disappeared after such a length of time. But the following evidence suggests in favour of the turbidite hypothesis.

The MAP area has been subjected to a number of distinct turbidite events over the past 10,000 years, culminating in the most recent event 930 years ago (Thomson and Weaver, 1994). Several lines of evidence are consistent with the hypothesis of a turbidite effect. Firstly, macrofaunal abundance was very low at MAP, significantly lower than the other north Atlantic sites including the equally oligotrophic EOS site (Figure 5.3). Secondly, polychaete diversity at MAP was different to the other abyssal sites so far examined, in that it appears to be more highly dominated. Such high dominance could be consistent with a community recovering from disturbance. Thirdly, polychaete species composition at MAP was characterised by cosmopolitan and widespread species with a lesser proportion of apparently unique species than at other sites (Figure 6.29).

Against these facts must be balanced the observation that the megafauna (Thurston *et al.*, 1994) does not show lower than expected abundance at MAP. In addition, current understanding of recolonisation rates both in shallow water and the deep sea suggest that recolonisation can be rapid, even in areas where the disturbance has been quite large scale (e.g. the DISCOL Experiment (Borowski and Thiel, 1998)). However, Thrush *et al.* (1996) have suggested that large scale disturbances can take longer to recolonise, particularly if key structuring species are removed.

Observations and experiments on deep-sea recovery tend to be on a small scale with the exception of the DISCOL Experiment (Borowski and Thiel, 1998) and HEBBLE study (Aller, 1989). At DISCOL, the scale of the disturbance was about 10 km^2 and it was disturbed only once. The disturbance took the form of ploughing up existing pelagic sediment. Recolonisation occurred on a scale of months to years. HEBBLE measured a phenomenon which occurs over a considerably larger area — hundreds to thousands of km^2. Disturbances are in the form of erosion and deposition of pelagic sediment. The frequency of the disturbance varies with the magnitude from nearly annually for large magnitude currents in excess of 25 cms^{-1}, to every 21 days for weaker flows (Aller, 1989). Such disturbances stimulate bacterial activity that can rapidly respond to localised inputs of labile POM during and after the deposition of eroded sediment. Most of the recolonisation by polychaetes and other macrofauna may be by non-larval immigration (Aller, 1989). Even such a large scale phenomenon appears to have a localised impact, such that not all areas are disturbed at any one time.

Both of these areas differ from the conditions at MAP in one major respect - the disturbance only reworks pelagic sediment, potentially releasing nutrients or stimulating microbial activity. At MAP the disturbance removed or overlaid existing sediment with a much coarser layer of allocthonous material derived from outside the abyssal basin. If abyssal macrofauna are influenced by sediment type - as suggested by Etter and Grassle (1992) - then recolonisation is likely to have been only possible when pelagic sediment was present or by organisms with wide tolerances. The dominance of cosmopolitan species at MAP may be a reflection of this. Also the DISCOL experimental area was much smaller in extent than the area of MAP subjected to turbidite flow. The area involved at MAP is greater than 2000 km^2.

The potential of an effect on the macrofaunal community structure even so long after the disturbance event cannot be discounted. Further analysis of fauna from different areas of MAP and surrounding regions would help establish just how localised these observations are.

In support of the turbidite hypothesis, a recent study has suggested that nematode diversity is also depressed at MAP (Lambshead *et al.*, in press). Again, the data suggest that the important factor is a long term change in sediment characteristics, caused by the turbidite, inhibiting the recolonisation of the turbidite sediments. Another possible explanation is that the limited dispersal abilities of nematodes have prevented recolonisation of this large disturbed area. For polychaetes, with potentially longer-lived pelagic larvae, it seems unlikely that the larvae would not have been able to reach the entire region in just a few years. More likely is the idea that the low sedimentation rates, coupled with low food input and an altered sedimentary regime has prevented larvae from settling and growing.

These results suggest that turbidites may have far-reaching effects on ocean basin margins and abyssal plains. A long-lasting impact over an area greater than 2000 km^2 in extent hints at the possibility that turbidites may have evolutionary as well as ecological significance. While there is now a greater understanding of the processes that maintain diversity in the deep ocean, such as the spatio-temporal mosaic theory, the mechanisms of speciation are still unknown.

Sanders (1968) suggested that the great stability of the deep-sea over long periods of time has allowed speciation to occur. But more recent studies have suggested that the deep sea is not the stable environment it once was. Such instability has been shown for very long time scales, and for very short ones. On long time-scales, over millions of years, there have been periods of anoxia and extinction in the deep-sea, most recently at the end of the Cretaceous and start of the Palaeocene (Rogers, 2000). On very short time-scales, over a matter of months and years, there is instability in terms of food availability and small-scale disturbance, as can be seen at the EqPac and Porcupine Abyssal Plain phytodetrital sites.

The turbidite hypothesis suggests that there may be a further scale of instability in the deep-sea, on scales of thousands of years. Turbidites are known to be caused by both long-term changes in climate (thousands to millions of years) and shorter-term events such as earthquakes (Weaver *et al.*, 1987). There was a well-known turbidite event off the Grand Banks caused by an earthquake in that region in 1929. It seems probable that the Madeira Abyssal Plain turbidite was triggered by an earthquake, although no historical record of this has been demonstrated. If turbidites lead to widespread disturbance and localised extinctions over large areas of abyssal plain, on scales of hundreds to thousands of years, then it is likely that they may be sources of geographical isolation and allopatric speciation.

Scales of natural disturbance in the deep-sea are summarised in Table 6.9. At small scales, bioturbation and small-scale disturbances, encourage the maintenance of diversity through the limitation of competition. Data from the HEBBLE site on the Scotia Rise, north-west Atlantic indicates that sediment resuspension on a scale of days causes a reduction in macrofaunal diversity and increased dominance (Thistle *et al.*, 1985). On seasonal and inter-annual scales, phytodetrital blooms lead to spatio-temporal heterogeneity. At larger scales, turbidites caused by earthquakes generate localised disturbance and extinction events, and geographical isolation, promoting speciation. At even larger scales, periods of climate change and sea-level alteration generate extended periods of turbidity currents possibly of extent great enough to lead to extinction rather than speciation. Finally, at the largest time-scale, deep-sea anoxia events associated with changes in the size of polar ice-caps lead to widespread abyssal extinctions, and reinvasions from bathyal refugia (Lipps and Hickman, 1982; Rogers, 2000).

Type of disturbance	**Time scale**	**Example**	**Significance**
Bioturbation	Hours to days	Porcupine Abyssal Plain	Ecological (diversity maintenance)
Sediment Resuspension	Several days	HEBBLE site, Scotia Rise, north-west Atlantic	Ecological (increased dominance)
Phytodetrital pulse	Seasonal / months-days	Porcupine Abyssal Plain	Ecological (diversity maintenance)
Phytodetrital pulse	Inter-annual / months-years	Equatorial Pacific - El Niño	Ecological (diversity maintenance)
Turbidity currents – earthquakes	Hundreds to thousands of years	Madeira Abyssal Plain	Ecological (disturbance) and Evolutionary (speciation)
Turbidity currents – sea level changes	Thousands to millions of years	Madeira Abyssal Plain	Evolutionary (extinction and/or speciation?)
Abyssal anoxia	Millions of years	Early Palaeocene extinctions	Evolutionary (extinction - bathyal refugia etc.)

Table 6.9 Scales of natural disturbance in abyssal ecosystems.

6.4.4 Regional enrichment of local species diversity in the Equatorial Pacific

The two variables so far discussed, productivity and disturbance, may explain some of the variation in local diversity in the abyss. But there is a further perspective – a historical one. The historical perspective is that of regional enrichment (Ricklefs, 1987). In the regional enrichment model, local, alpha diversity is reliant both on local ecological processes such as productivity-disturbance and regional influences such as the total pool of potential colonisers. Regional-historical processes determine how many species are available. Local processes determine how many of those species can live at a single point. Local diversity represents a balance between local extinction processes and colonisation from the regional species pool.

Historically, community ecologists have focussed on local processes rather than historical ones (Ricklefs, 1987). The 'great leap forward' of ecological diversity work in the 1960's and 70's was based mainly on local processes. Ecologists concentrated their efforts on understanding how communities were influenced by predation, competition and patchworks of physical disturbance, culminating in the ecological paradigms of the intermediate disturbance model (Connell, 1978) and the dynamic equilibrium model (Huston, 1979).

The regional enrichment model hints that there is more to local diversity than the models of MacArthur, Connell and Huston. Underpinning the idea of regional enrichment, is the concept of community saturation (Cornell, 1993). By analogy, a box filled with balls will be saturated if no new balls can be added. An unsaturated box is one where the balls can be compressed to make room for new additions. In an ecological sense, the sensitivity of a site to regional enrichment will be dependent on community saturation. Saturated species assemblages are those where local diversity is not influenced by changes in the regional-historical pool of species. In contrast, unsaturated assemblages are those where local diversity can be propped up by the regional species pool.

> *"A growing body of evidence indicates that many communities do behave as unsaturated assemblages of species..."*
>
> \- *Rex et al. (1997)*

It was originally hypothesised in Section 2.4 that the Pacific ocean, with its greater area and longer history, is likely to have a greater regional species pool than the Atlantic ocean. Following on from this, sites in the equatorial Pacific, comparable in other respects to north Atlantic sites, can be hypothesised to have higher local diversity, assuming them to be unsaturated. In the analysis (Figure 6.11), this was indeed born out. Pacific phytodetrital sites supported 25% more species for equivalent numbers of individuals than north Atlantic ones.

It should be emphasised that an analysis of only two sites is limited in scope – but this result provides tantalising evidence that abyssal assemblages may be sensitive to regional enrichment. The regional diversity of the Pacific abyssal polychaete fauna is unknown, so it remains conjecture to suggest that it is higher than in the Atlantic. But the Pacific is well known as being a hot-spot of biodiversity for shallow-water fauna, owing to its area, age and the physical 'archipelago' nature of the coast (Stehli and Wells, 1971; Karlson and Cornell, 1998; Karlson and Cornell, 1999). Furthermore, primary importance has been suggested for both area and age as explanations for high diversity in other systems (Rohde, 1992; Rosenzweig, 1995). The Pacific Ocean has an area of 166 million km^2 as opposed to 82 million km^2 in the Atlantic. And the oldest rocks in the Pacific date back to 200 mya, as against 150 mya in the Atlantic. In fact, the Pacific Ocean is even older than these dates suggest, and is distinct from the Atlantic in that it was formed well before the break up of the Pangaea in the Permian. It is not an unreasonable assertion that the Pacific may have a higher regional species pool than the Atlantic.

Only one other study has looked for evidence of regional enrichment in the deep-sea (Stuart and Rex, 1994). In that study, of deep north Atlantic prosobranch gastropods, a positive correlation was shown between regional diversity and local diversity, indicating that deep north Atlantic assemblages are unsaturated. Stuart and Rex (1994) also examined the larval shell morphology of these deep-sea gastropods to investigate the predominant mode of dispersal. Deep-sea invertebrates such as gastropods and polychaetes may reproduce through larval dispersal in the water column (either by planktotrophic larvae or lecithotrophic larvae), or via direct non-planktotrophic development where young are hatched crawling. They discovered that the proportion of planktotrophic developers was correlated with regional enrichment, further supporting the idea of unsaturated assemblages in the abyss. In sites that were particularly susceptible to regional enrichment, the highest proportion of planktotrophic-mode species were found.

The results of this study, and that of Stuart and Rex (1994) indicate that deep-sea sites may well be unsaturated. The implications of this are that deep-sea ecologists can no longer afford to ignore the imprint of historical contingency. In recent years, the great discoveries in deep-sea biology have been in the field of small-scale process; through experimentation and fine-scale sampling, ecologists have unearthed the paradigm of spatio-temporal heterogeneity as the main theoretical underpinning of diversity. But to understand why one place is more diverse than an other, which is assuredly the ultimate goal of many ecologists, a broader regional, historical and biogeographical knowledge is required.

For the purposes of this study, limited data are currently available to follow up the observations of regional enrichment in the Pacific. There has been little or no work on the reproductive biology of deep-sea polychaetes; considering the breadth of polychaete reproductive modes in shallow water (Wilson, 1991; Morgan *et al.*, 1999), there may yet be a wealth of data to uncover from the deep sea. However, one line of analysis may help to elucidate regional patterns of diversity – an investigation of beta diversity patterns. The regional enrichment observations in the central Pacific suggest that polychaetes will have broad distributions, and limited endemism. Quantifying the degree of faunal turnover is a first step towards a biogeography of the abyss, and a biogeography of the abyss may well be what is required to fully understand the patterns of local diversity.

6.4.5 Patterns of beta diversity in the abyss

The rate of species accumulation with area could be construed as a measure of beta diversity, although it is inherently sample-size dependent (Figure 6.13). A central problem throughout the analysis of beta diversity was teasing out real faunistic differences, and those caused simply by differences in abundance (and hence sampling intensity). But there is some evidence to suggest that species were accumulating with area at a faster rate at the EqPac phytodetrital sites compared to the Atlantic phytodetrital sites, which have a similar sample size. This may be caused by higher sample diversity at the EqPac phytodetrital sites, as indicated by the rarefaction analysis (Figure 6.11).

The nature of the species accumulation curves attests that for most of the sites, not all of the species have been found. In a terrestrial-style study, one of the reasons for looking at species accumulation curves is to determine the point at which the habitat has been adequately sampled. One of the major problems in applying such terrestrial-style community analysis to the abyss is that defined habitats and communities may not actually exist. The only definable 'community' may in fact be a sample – continue sampling and species will accumulate until the entire deep-sea species pool is eventually sampled.

An investigation of the faunal similarity of sites over different areas was pursued in order to test whether the deep sea is one homogenous province, or consists of real, definable communities. The Kulczynski analysis of faunal similarity indicated that as sampling intensity increases, faunal similarity between two sites also increases, irrespective of the distance between the two (Table 6.2; Figure 6.14). This does not support the hypothesis that there are real communities and habitats in the abyss. Even if the sites are under-sampled, some effect of distance, and/or phytodetrital regime, would be expected if there were real community differences between the sites.

Continuing this analysis with the supposedly sample-size independent similarity measure, NESS, indicates again that there are no obvious clusters related to phytodetrital input, sedimentary regime, or simple distance effects. The EqPac phytodetrital sites cluster together based on sampling intensity (Figure 6.16). At the manganese nodule sites, ECHO 1 and PRA cluster within the overall DOMES A cluster, indicating that the intensity of sampling is such at DOMES A that the ECHO 1 and PRA sites are merely subsets of this fauna (Figures 6.17; 6.18). In the north Atlantic, the intra-site variability is as great as the between-site variability, clustering is again principally determined by sample-size. The MAP site forms a separate cluster when only the dominant species are investigated (at $m=5$) supporting the hypothesis put forward in section 6.4.3 that physical disturbance has led to high dominance at this site. In summary, the NESS similarity index is actually highly influenced by sample size, as demonstrated conclusively in Figure 6.22. The mean sample size of the two sites being compared is a much better predictor of NESS similarity than distance, or differences in productivity.

The ecocladistic analysis actually provides a better example of the patterns regarding beta diversity. In Figures, 6.23 (EqPac) and 6.25 (Atlantic), what is remarkable is the huge number of endemic species at each site – as indicated graphically in Figure 6.26. But at the more intensely sampled manganese nodule sites (Figure 6.24), which are separated by similar distances to the EqPac and Atlantic sites the ratio of endemics to cosmopolitan species is much lower – there are many more cosmopolitan species. The quantification of the ecocladistic data – in Figures 6.27, 6.28 and 6.29- only shows what is already suspected, that cosmopolitan species are extremely abundant at all sites, and that a large amount of the diversity at each site is composed of very low abundance endemic species. The fact that at the manganese nodule sites, the proportion of cosmopolitan species, and the proportion of individuals that are cosmopolitan, both increase dramatically is indicative that the superficially high endemicity of the EqPac and Atlantic sites (Figure 6.23 etc.) is a result of undersampling. Sample diversity in the abyss is propped up by a long tail of rare species. Increases in sampling intensity reduce the tail of endemics, and their importance is diminished (Figure 6.28).

These slightly confusing signals at species level are more transparent at family and functional level (Tables 6.5; 6.6; Figure 6.30). Although it was not viable to compare oceans at species level, this was possible at a family and functional level. Fundamentally, there is very little change in familial composition between sites, regions and oceans, with the same families dominating throughout. Unsurprisingly, this is also reflected at functional level, as functional group assignments are dependent on family.

There was, however, one potentially significant trend in the family level data (Table 6.5). In the north Atlantic, the dominant predatory family was the Pilargidae; in the Pacific it was the Syllidae. Both species occupy similar functional roles (Fauchald and Jumars, 1979). This result hints at a potential oceanic level of beta diversity, that may be of great consequence to measurements of total biodiversity. Further work on species level similarity between the Pacific and Atlantic oceans would be required to confirm this observation, possibly requiring a molecular level analysis.

The significant conclusion of this analysis of beta diversity is that at scales up to 3500 km, there is very little habitat or community partitioning in the abyssal ecosystem. Differences between sites are the result of undersampling, and the long tail of rare species, rather than real changes in faunistic composition.

There has been only limited recent work on abyssal beta diversity, or even of broader scale biogeographic patterns, with which to compare and evaluate this assertion. R.Y. Levenstein has worked on the extensive abyssal collections of the former Soviet Union, in 1972, she published a paper on the ecology and zoogeography of some of these abyssal polychaete species (Levenstein, 1972). Of particular interest were species of the genus *Macellicephala* (Aphroditidae), of which there are about 17 abyssal representatives. Tellingly, she wrote in 1972:

> *"Thus the conclusion concerning the predominance of narrow-localised distributions among the species of the genus* Macellicephala *should be handled with extreme care... it is natural to expect that the ratio between the number of localised abyssal species and cosmopolitan species will change as studies of the deep-sea bottom fauna become more and more intensive."*

Levenstein (1972) demonstrated that many of the species of *Macellicephala* were shown to have panoceanic distributions, as well as several species of the exclusively deep-sea family Fauveliopsidae. Other widespread species indicated were the opheliids *Kesun abyssorum* and *Travisia profundi*, present in all three oceans, and the Antarctic.

Recently, Kirkegaard (1994) has reviewed the biogeographical distribution of abyssal polychaetes collected aboard the famous Danish Galathea expedition (1950-52). His conclusions that many of the species showed panoceanic cosmopolitan distributions were in agreement with the earlier results of Levenstein (1972). Original type material was re-examined, and for the aphroditid *Laetmonice benthaliana*, a widespread distribution across the central Pacific, Indian Ocean and Antarctic was indicated. The sigalionid, *Leanira quatrefagesi* was shown to occur in all oceans, and the Antarctic. Out of the six species investigated, four were shown to have worldwide distributions, and two were widespread across at least two oceans. Kirkegaard concluded that '*...there is very little variation in morphology and size over large geographical distances*'.

Most of the abyssal species examined by Levenstein and Kirkegaard were those collected using trawls and large mesh sizes – from high productivity areas of the abyss such as upwelling zones. Oligotrophic gyre regions were not intensively sampled. For this reason, in these older studies, a quite different polychaete fauna was examined – the large scavenging megabenthic scale worms are not normally collected in box cores (see section 5.3.2). The data in this study indicate that for the smaller infaunal polychaetes, similar widespread distributions occur in the abyss, at least on scales of up to 3500km. The little variation in familial and functional group composition between oceans suggests that the pattern may be repeated on a panoceanic scale.

In shallow-water systems, many supposedly cosmopolitan species have been shown to be based on inadequate descriptions or lack of comparison with type specimens. This has resulted in many such species being split up into several species with more restricted distributions. But the data from the abyss suggests that this may not be true of abyssal species. This result does not agree with the findings of Paterson *et al.* (1998) who suggested that faunal turnover may be operating on 1000km scales. The abyssal oceans are connected physically, albeit over large distances, and assuming planktotrophic reproductive modes it is easy to see how polychaetes may show very wide distributions, associated with prevailing ocean currents.

The data on beta diversity support the hypothesis put forward in the previous section (6.4.4) that regional-historical processes are significant in shaping local alpha diversity patterns. If polychaetes have wide distributions, with planktotrophic modes of reproduction, then the regional pool of species is likely to have a much larger impact on local diversity. Unsaturated assemblages are likely to be more susceptible to variation in regional diversity. Two lines of inquiry are needed to confirm this finding. Firstly, the question of reproductive mode and dispersal ability for abyssal polychaetes must be addressed. Secondly, molecular work on cosmopolitan species would resolve the question of whether the abyssal fauna is unique in its cosmopolitan pattern of species distributions – or whether allegedly cosmopolitan species are in fact much more restricted.

6.4.6 Conclusions

Polychaete species diversity in the abyss is initiated and sustained by a patchwork of spatial and temporal processes. On small scales, productivity and disturbance and the spatio-temporal mosaic theory lead to the ecological maintenance of diversity. At larger scales, natural physical disturbances caused by turbidites influence the diversity of ocean basin margin sites both ecologically and perhaps evolutionarily. Potentially widespread species distributions in the abyss hint at the importance of regional processes; the dependence of local diversity on regional-historical contingency cannot be overlooked. The Pacific ocean, larger and older than the Atlantic, shows higher species diversity, supporting the theory of regional enrichment. To understand species diversity, a wider biogeographic and systematic knowledge is required. Recent advances in our understanding of biogeography and systematics, through cladistic methods and molecular tools, should be applied to the problem of comparative species diversity in the deep sea.

6.5 Summary

- Simple species counts per unit area are not a suitable way of quantifying species richness of polychaetes in the abyss as they are highly density-dependent.

- Density-independent measures of species diversity, sensitive to both richness and equitability, are larger in EqPac phytodetrital sites compared to more oligotrophic Pacific sites.
- Diversity at the EqPac phytodetrital sites is enhanced by a combination of increased productivity, spatio-temporal patchiness of food distribution, small-scale disturbance by bioturbating animals and increased sediment size heterogeneity.
- In the north Atlantic, there was no support for the hypothesis that phytodetrital sites are more diverse than non-phytodetrital ones, although the pattern is confused by possible terrigenous influences such as large scale turbidite emplacements and the influence of west African upwelling.
- At the MAP site in the north Atlantic, large-scale natural disturbance has reduced species diversity over a large area, greater than 2000 km^2. Disturbance at a variety of spatial and temporal scales is responsible for both the ecological maintenance of diversity, and the promotion of allopatric speciation.
- In the central Equatorial Pacific, local diversity is enhanced by the high regional pool of species in the Pacific, caused by its greater areal extent and age. Regional-historical processes may be significant in shaping local diversity patterns in the abyss.
- Investigations of beta diversity were confounded by sample-size dependence. Ecological cladistics and a simple analysis of the abundance of cosmopolitan species indicates that on scales of up to 3500km, and across significantly different productivity regimes, there are no clear community boundaries. This supports the idea that regional processes may be significant in shaping local diversity.
- Historical research on the collections of early Soviet and Danish expeditions supports the idea that abyssal polychaetes do not show restricted distributions. Further work on reproductive biology and molecular level analyses is probably needed to confirm this observation.

7 ABYSSAL POLYCHAETE ECOLOGY: RELATIVE ROLES OF LOCAL AND REGIONAL PROCESSES

7.1 Introduction

The preceding chapters of this thesis provide convincing evidence that abyssal polychaete assemblages are structured by both local and regional processes. In this chapter, this concept is explored further, and a locally deterministic approach avoided. 'Local determinism' may be usefully defined as seeking to explain local patterns of ecology using local processes only (Ricklefs and Schluter, 1993). Research in ecology over the last thirty years has been driven by this local determinism, while researchers working on the regional patterns of evolution and biogeography have, by and large, pursued a separate avenue of research. The question of species diversity is an excellent example of how the same enigma has been attacked using two quite different approaches.

On the one hand, ecologists have concentrated on seeking to explain the patterns they see with respect to the processes of local population biology in the general framework of extinction, competition and predation (Huffaker, 1958; Hutchinson, 1959; Paine, 1966; Connell, 1978). On the other hand, there has been the cladistic revolution in the understanding of systematic and biogeographic patterns, and the evolutionary and historical reasons for them (Ridley, 1986). Both fields have led to remarkable improvements in our understanding of the patterns of species diversity. Ecologists, through both pattern-based and experimental work have elucidated the main forces involved in the ecological maintenance of diversity, at small scales. Systematists, by analysing species relationships using morphological and molecular tools, have unearthed the inherent phylogenetic constraints of diversity; the historical contingency upon which ecology must operate.

Scientists are fond of espousing the value of scientific synthesis. Entire disciplines of biology, such as landscape ecology, are based on the premise of emerging properties with a holistic approach (Forman and Godron, 1986). The problem of the holistic approach is coming up with useful theory in the face of great complexity in observation. There is a danger of belittling the great discoveries that have been made using small-scale observation and hypothesis-testing. Much of our knowledge of process, with regard to deep-sea diversity, has been led by small-scale studies (Smith, 1986; Grassle and Morse-Porteous, 1987). But the resurgence of interest in large-scale diversity patterns, led by ecologists, does require a confluence of ecology and evolution. In addition, the growing body of evidence that local species assemblages are influenced by regional diversity indicates that even small-scale ecology cannot ignore larger-scale processes.

Ricklefs and Schluter (1993), in the light of these observations, made five suggestions for the future of ecological research: (1) that the phenomenon of diversity itself be better characterised, in particular the spatial scale of diversity being measured; (2) that relationships between these scales of diversity be explored, in particular the dependence of local diversity upon regional diversity; (3) that studies should investigate the development of species assemblages through the incorporation of their systematic and evolutionary history; (4) that ecologists should explore the role of speciation and extinction to determine whether the intrinsic properties of species and habitats are related to patterns of regional diversity and (5) that investigations of the adaptive radiation of species into new habitats be carried out, using analyses of morphology and molecular data.

Part of the purpose of this chapter is to investigate to what extent these lines of inquiry can be pursued in the deep sea using the limited datasets available. A number of unanswered questions remained at the end of the previous chapter, which, as will be seen, require a more holistic outlook. Firstly there was the question of productivity, which showed a strong influence on species diversity in the Pacific Ocean, but not in the Atlantic Ocean. Secondly there was the effect of large-scale disturbance in the north Atlantic, which appeared to have impacted species diversity over a potentially vast area. Thirdly, there was the observation that high local diversity at EqPac may be related to high regional diversity in the Pacific Ocean as a whole, in agreement with the results of Stuart and Rex (1994). Finally, the analysis of beta diversity indicated that there may be very low rates of species turnover across large distances in the abyss.

This chapter follows the following format. In the first section, local patterns of diversity, and local processes invoked to explain them are revisited in the light of observed patterns and influences of regional diversity. In the second section, a combined local and regional perspective is applied to the question of total deep-sea diversity for abyssal polychaetes. In the final section, the propositions of Ricklefs and Schluter (1993) are reviewed, and potential evolutionary and ecological studies suggested.

7.2 The Productivity Paradox in the Abyss: Local Patterns, Regional Processes

In the central equatorial Pacific, species diversity, as measured by indices sensitive to both richness and equitability, was highest in the food-rich phytodetrital sites lying under high productivity upwelling zones. There was an approximate 30% increase in diversity at these sites, compared to sites in the more oligotrophic regions lying under the central oceanic gyre.

In the previous chapter, four hypotheses were put forward as to why this pattern might occur: (1) increased productivity *per se* at the food rich sites increases diversity by reducing the effects of accidental extinction on rare species, allowing a longer tail of rare species (Rosenzweig and Abramsky, 1993); (2) increased spatio-temporal patchiness of food availability increases diversity by permitting the existence of a mosaic of successional states (Grassle and Morse-Porteous, 1987); (3) increased disturbance generated by bioturbating organisms such as large urchins generating greater small-scale environmental heterogeneity (Connell, 1978; Grassle and

Morse-Porteous, 1987); (4) greater sediment heterogeneity at the phytodetrital sites (Etter and Grassle, 1992). Note that many of these hypotheses are not mutually exclusive; productivity on its own may ultimately be responsible for the other three hypotheses.

The observation of high species diversity at EqPac, supports the previous hypothesis of Grassle and Morse-Porteous (1987), and, in a true abductive sense (see section 2.1) generates four new hypotheses. It is not apparent which of these four hypotheses has the most explanatory power – but it seems probable that they all may play a part. Although experimental studies are the only way of demonstrating the precise controls on local species coexistence, the patterns of local and regional diversity in the Pacific and Atlantic help to indicate the relative roles of the various processes concerned.

The observation of enhanced local diversity at phytodetrital sites was not observed in the north Atlantic. One explanation might be a difference in local ecology between EqPac and PAP. But there are no obvious differences in habitat conditions between the PAP and EqPac 0°N-5°N sites. Both lie under high productivity regimes, with significant inputs of phytodetritus, and an active bioturbating surface fauna. POC flux is slightly lower at PAP than at EqPac (1 $gCm^{-2}yr^{-1}$ versus 1.6 $gCm^{-2}yr^{-1}$) but the differences are not as great as that between PAP and EOS, or EqPac and the manganese nodule region. Functionally, there are no significant differences between the PAP fauna and the EqPac fauna, indicating that there is not a shift in community composition.

In Chapter 5 it was shown how the north Atlantic sites are less tightly coupled to measures of surface productivity than the central Pacific sites, when measures of abundance are considered (Figure 5.6). The significant finding of Chapter 6 may be that in terms of species diversity, the relationship between productivity and diversity is also confused in the Atlantic. This is in agreement with the results of the analysis of nematode datasets (Lambshead *et al.*, 2000). Lambshead indicated that much of the variability in species diversity was related to the local ecological conditions of the separate ocean basins, rather than any clear productivity-based or latitudinal relationship.

One possibility is that the oligotrophic EOS site, which was used as a low productivity site with which to compare PAP, is not as oligotrophic as indicated by the measurements of POC flux. Inter-annual variability in productivity is unknown at EOS; the recent data from the *SeaWifs* satellites indicates that there may be considerable variation in the size of west African upwelling. Some studies have looked at the variability in surface pigment concentrations using the CZCS data, indicating that considerable variation may occur inter-annually in response to El Niño events in the area surrounding the Canary Islands, close to EOS (Hernandez-Guerra and Nykjaer, 1997). Furthermore, although the EOS site does not lie directly underneath the upwelling zone, there remains the possibility that downslope processes, which are extremely common on the west African continental slope may contribute significantly to overall organic input (Weaver *et al.*, 2000). While erroneous POC measurements at EOS remain a possibility, such fitting of fact to assertion should be treated with caution. The influence of regional processes may explain why diversity at EqPac 0°-5°N is so high.

> *"...the influence of regional and historical factors becomes apparent when local species richness in a given habitat type differs between regions"*
>
> *- Ricklefs and Schluter (1993)*

In the previous chapter, it was hypothesised that high regional diversity in the Pacific may be responsible for increased local diversity at the EqPac phytodetrital sites. This finding was in agreement with that of Stuart and Rex (1994) who suggested that the local diversity of deep-sea prosobranch gastropods was significantly correlated with regional diversity.

One of the central problems in demonstrating the dependence of local diversity on regional diversity is actually being able to measure both types of diversity independently. Local diversity may be dependent on regional diversity, but regional diversity may itself be dependent on the sum of the local diversities within it. As Cornell (1993) puts it, *"...is local richness the dependent variable...or should the axes be reversed, making regional richness the dependent variable?"* It is not known what the regional diversity of the Atlantic and Pacific oceans is, but given that species diversity increases with area, and that this pattern is one of the most universal in all nature, it is reasonable to suppose that regional diversity is significantly higher in the Pacific.

What may be crucial to resolving the productivity paradox is to understand that in the deep sea, species assemblages may be unsaturated. That is, given a larger pool of potential colonisers, local diversity is enhanced by the presence of this larger general species pool. In terrestrial studies this has been demonstrated for some communities, in particular those of insects on host plants (Lawton, 1984). In the deep sea, Stuart and Rex (1994) hypothesised this for north Atlantic gastropods. In a review of deep-sea diversity data, Snelgrove and Smith (in press) put forward a closely related argument that species rich areas may provide a source of species for less rich ones.

Assuming that deep-sea species assemblages are unsaturated, it may be possible to explain the observed patterns at EqPac. At the phytodetrital sites, local processes encourage high species diversity, but crucially, the large regional species pool of the Pacific is the ultimate source of that diversity. In the north Atlantic, diversity at the food-rich PAP site is enhanced by local processes, but at the same time it is also limited, in comparison to EqPac, by the smaller pool of potential colonisers. Local processes, encouraged by spatio-temporal heterogeneity, high productivity and sediment diversity result in assemblages that are unsaturated, and open to invasion by new species. The unsaturated nature of the assemblage means that these new invaders increase species diversity, rather than simply replacing species that are already there. By analogy with the balls in the box scenario, the balls at both EqPac and PAP are both squashable, but at EqPac there are more balls.

The significant finding here may be that as Lambshead *et al.* (2000) put it, the Atlantic Ocean may be the 'wrong ocean' for large-scale studies of diversity patterns. Local ecological processes in individual ocean basins may be responsible for much of the observed diversity patterns in the north Atlantic. In the central Pacific, where terrigenous influences are less apparent, and there is much tighter coupling of benthic-pelagic process (Chapter 5), there is closer agreement between diversity and productivity. Regional enrichment augments this relationship; where there is space for more species, there are more species available. Further support for this argument is found when one considers the impact of large-scale natural disturbance in the north Atlantic.

Reduced diversity and increased dominance at the Madeira Abyssal Plain site was hypothesised to have been caused by a large-scale turbidite emplacement 1000 years in age. This surprising observation has been supported by data from an analysis of nematode assemblages (Lambshead *et al.*, in press). What is significant is that this is a disturbance on a much larger scale than that which is usual in a local ecological situation. The data do not, however, suggest that the disturbance is so extensive as to reduce regional diversity at MAP. The analysis of faunal composition indicated that the same range of species were abundant at MAP as at the other north Atlantic sites, although there was a much greater relative abundance of cosmopolitan and widespread species. Given the hypotheses put forward regarding the widespread distributions of polychaete species (section 6.4.5), it is unlikely that there are fewer potential species available to colonise sediments at MAP. The most likely explanation is that the local conditions at MAP – altered turbidite sediments – have prevented recolonisation of fauna that is, at least, able to reach the area. The disturbance is a local ecological influence that is widespread at a 2000 km^2 plus scale.

What is significant from the results of the north Atlantic study is that a new scale of disturbance has been highlighted, on what can be termed a 'landscape' scale. In the classic text on the terrestrial discipline of landscape ecology, Forman and Godron (1986) define the landscape as 'a heterogeneous land area composed of a cluster of interacting ecosystems which is repeated in similar form throughout its kilometres-wide extent'. In the deep north Atlantic, individual ocean basins represent the landscapes within which local population and metapopulation processes influence local diversity. Including this disturbance pattern within the general framework of deep-sea disturbance patterns (Figure 7.1) indicates how a continuum of disturbances across spatial and temporal scales influence diversity patterns at both ecological and evolutionary levels.

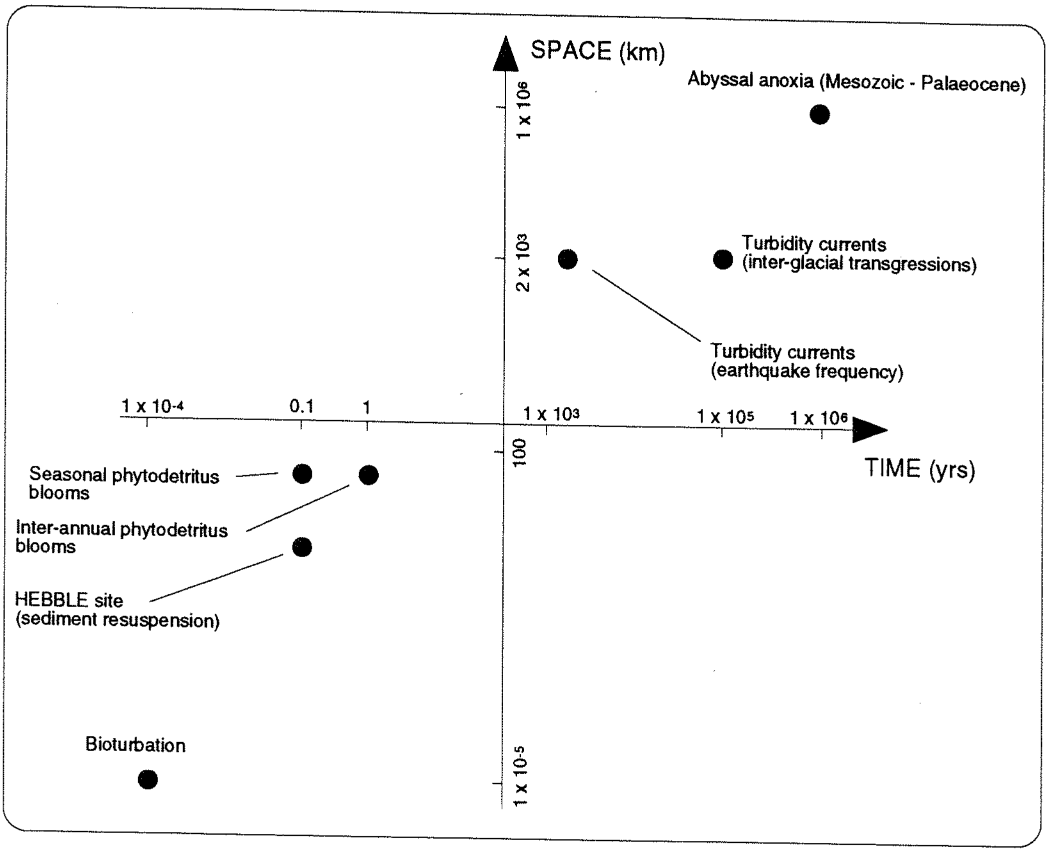


Figure 7.1 Spatio-temporal scales of disturbance in the abyssal ecosystem.

Ecologists have spent many years struggling to come to terms with the productivity-diversity relationship. In keeping with this trend, no simple clue to its cause comes from these deep abyssal sites. Possibly the best way to understand the paradoxical patterns from the two oceans is to think of the abyss as an experimental zone. In experiments, the investigator strives to keep all other variables equal except the one of interest to the study. In an investigation of productivity, an experimental approach would attempt to reduce all other influences, such as that of disturbance and un-quantifiable organic input, while monitoring sites following simple manipulations of food input. This was the procedure used in the classic studies of nutrient enrichment in plant communities (Tilman, 1982). The EqPac transect is as close as it comes to pattern-based experiment, while the clue to the productivity paradox of the deep north Atlantic lies under a blanket of confounding variables.

7.3 Total Abyssal Polychaete Diversity: Local Clues to Regional Patterns

> *"It is a popular delusion that the scientific enquirer is under an obligation not to go beyond generalisations of observed facts...but anyone who is practically acquainted with scientific work is aware that those who refuse to go beyond the facts, rarely get as far."*
>
> *- T.H. Huxley*

Nothing could be more appropriate in deep-sea biology than Huxley's quote on the value of speculation. Paterson (1993) estimated that less than 2 km^2 of the sea-bed has been accurately sampled for macrofaunal organisms. Given that the total areal extent of deep-sea ecosystem below 2000m is 270 million km^2, a lot of observation, hypothesis, theory and speculation has arisen from a very small sample. A popular line of speculation is total species richness, or the total number of species in the deep sea.

The total species richness debate began in terrestrial ecology. In the early 1980's, Erwin (1982) sampled 1200 species of coleoptera on a single species of the tropical rainforest tree, *Luehea seemanii*. Erwin estimated that 13.5% of those beetles lived only on that particular species of tree, and assuming that level of endemicity on all tropical tree species (all 50,000 of them) produced a figure of 8.1 million species of beetles specialising on single tree species. Erwin then added in the number of species living on several tree species, 2.7 million of them, bringing the total up to 10.8 million species of beetle. Further extrapolating, he suggested that if beetles represent about 40% of all arthropods, then there are about 27 million species of arthropods in the tropics. Adding this to the figure of 3 million temperate species produced the final, often cited, 30 million arthropod species in the world.

A number of recent reviews have revised Erwin's estimates both upwards and downwards (e.g. May, 1990). In the marine realm, there has been considerable interest in deep-sea diversity as a potential rival to that of tropical forests (Grassle and Maciolek, 1992; May, 1993; Gage and May, 1993; Poore and Wilson, 1993). Grassle and Maciolek (1992), in one of the most comprehensive surveys of deep-sea benthic habitats to date, estimated that there may be 10^7 species of macrofauna in the deep-sea. They reached this estimate by analysing the rate of species accumulation with increasing numbers of individuals along a 2100m depth contour of 176km in length. The crucial part of their analysis was the assumption of species accumulation with area:

> *"After the initial rapid increase in species as samples are added along the 176-km transect, the data in figure 11 suggest a rate of increase in number of species with distance on the order of 100 species per 100 km."*
>
> *- Grassle and Maciolek (1992)*

Given this observation, and assuming the rate to be held constant across the entire deep sea, results in extremely high estimates of total species richness. But this assertion was questioned by May (1993), who suggested that species replacement along global gradients is unlikely to be linear. Grassle and Maciolek (1992) indicated that 58% of the species they found were new to science. Assuming this, May (1993) suggested that the total number of species in the deep sea is unlikely to be more than twice that already described, or about half a million. In other words, twenty times less than the estimate of species richness made by Grassle and Maciolek (1992).

Poore and Wilson (1993) showed how benthic diversity of isopods faunas was highly variable between regions, but that overall, a figure of 22 species per 100 individuals was in fact a much higher estimate of diversity than that made for the same taxon by Grassle and Maciolek (1992). In addition, they pointed out the high species diversity of shallow marine habitats, and the significant contribution they make to global diversity. But May (1993) indicated that estimates of diversity such as the rarefaction method are significantly influenced by the evenness component of diversity, and are unsuitable when it comes to analysing regional patterns.

In this study, the analysis has been limited to abyssal polychaete assemblages at depths greater than 3500m. It is of use to attempt to estimate the diversity of this subset of the whole first, then attempt to compare it with firstly, estimates of macrofaunal diversity and secondly estimates of diversity from continental slope and shelf depths. Two important aspects of diversity must be understood before an estimate of abyssal polychaete diversity can be made. Firstly, a reasonable figure for within-habitat (alpha diversity) must be available. Secondly, an estimate for the degree of species turnover between habitats (beta diversity) is required.

The DOMES A site in the central equatorial Pacific is probably the most intensively sampled abyssal site to date. It is the only site where the species accumulation curve with area (Figure 6.13) shows any sign of leveling off. Hence, the DOMES A site is a reasonable candidate for an estimation of within-habitat alpha diversity. Even so, the number of species is obviously still increasing with increasing sampling effort, so some sort of estimator is required to generate a total habitat diversity figure. A simple method is to use the well-known relationship between species richness and area, extensively reviewed by Rosenzweig (1995). Given that the best predictor of species richness with area is based on a linear relationship with both axes in logarithmic space, the equation can be used:

$$Log\, S = z \log A + \log C$$

where S is the number of species, A is area, z describes the slope of the line and C the intercept. The equation can be simplified such that:

$$S = CA^z$$

This equation can be used as a predictor of species richness in a given area, once the relationship between species richness and area has been elucidated (Gray, 2000). There are two approaches, firstly to plot the data in log-log space and perform a simple linear regression to obtain values of C and z (Figure 7.2), secondly to plot the data in their raw form and perform a non-linear logarithmic regression (Figure 7.3) (Rosenzweig, 1995).

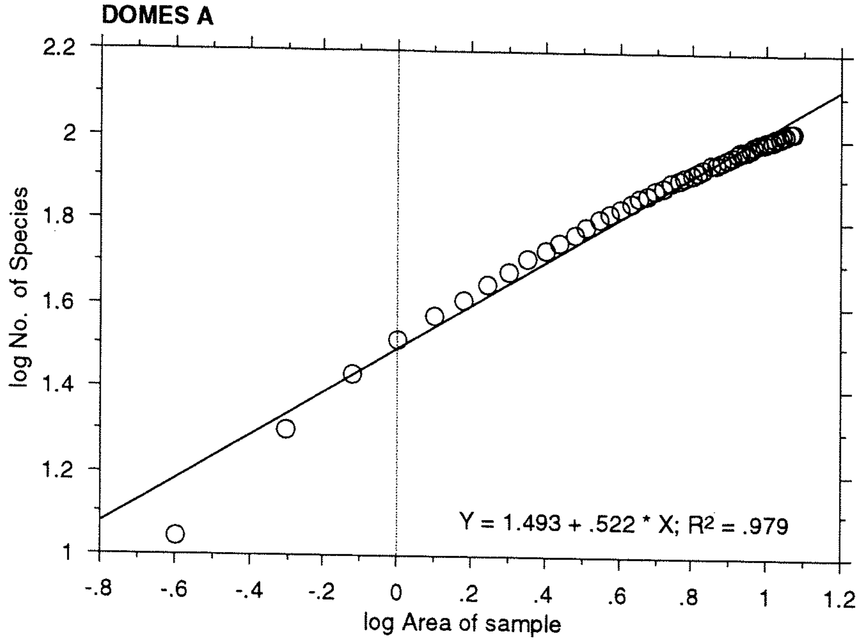


Figure 7.2 Species-area curve for DOMES A in log-log space with simple linear regression.

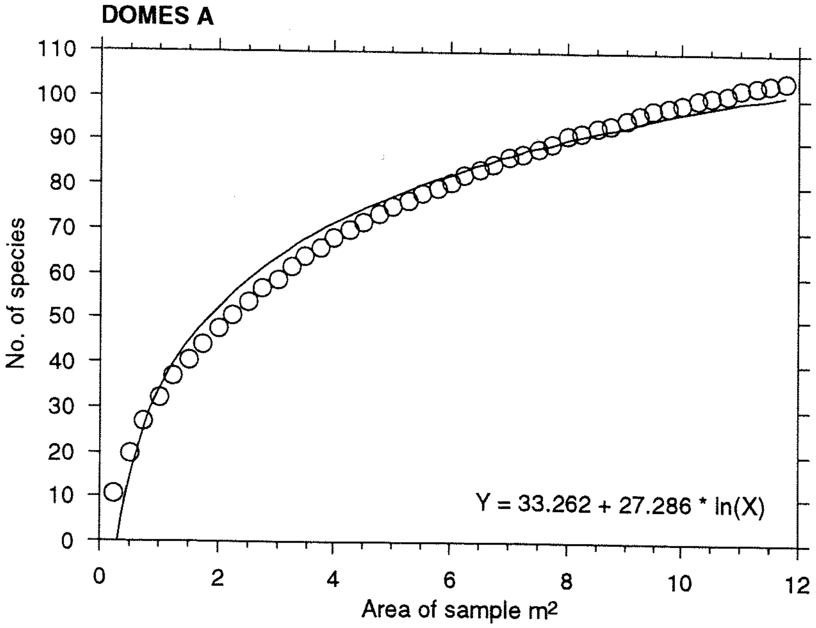


Figure 7.3 Species-area curve for DOMES A with non-linear logarithmic regression.

For both analyses, an estimate of species richness can be made for a given area using the equation of the line. From the nature of the fit between regression line and data, it is apparent that for the log-log model, species richness will be overestimated, and for the non-linear model, species richness will be underestimated. This is borne out in the results, for an estimation of species richness at 12 m^2 (the total area sampled), 50 m^2, 100 m^2 and 500 m^2 (Table 7.1). Species richness increases faster with area in the log-log model, and more slowly in the non-linear model. An estimate for species richness with 100 m^2 of sampling (equivalent to 400 box cores) is 343 species in the log-log model and 157 species in the non-linear model. Wright (1981) suggests that the non-linear model may provide a better estimate for the species-area relationship, although that was for an analysis of vertebrate species richness across archipelagos, which is hardly a comparable ecosystem. Rosenzweig (1995) points out that for a real species-area relationship to be measured, a nested sampling design should be carried out. Unnested designs, such as a deep-sea sampling study are likely to overestimate the slope *z* of the line, particularly in the log-log linear model, hence overestimating species richness.

Area	**No. Species (log-log model)**	**No. Species (non-linear model)**
12 m^2	113	100
50 m^2	238	138
100 m^2	343	157
500 m^2	794	200

Table 7.1 Estimates of species richness with area at DOMES A modeled using the species-area curve relationship.

Paterson *et al.* (1998) analysed the DOMES A dataset using the Chao 2 method (Chao, 1987). Species richness estimates appeared to level off at approximately 140 species, not far in excess of the 104 species that were actually discovered. The non-linear species-area curve model (Table 7.1) indicates similar levels of species richness. The estimates made using the log-log model are in excess of those made using Chao 2 and the non-linear model. This variability in species richness at DOMES A precludes an accurate estimate of alpha diversity, but it seems likely that total species richness at DOMES A does not exceed a few hundred species.

Conservatively assuming that abyssal alpha species richness is in the region of 100-500 species, the next logical step in the analysis is to determine the degree of faunal turnover, or beta diversity. There is no evidence to suggest that beta diversity is especially high for abyssal polychaete assemblages. The work on larger organisms carried out in the early 1970's (Levenstein, 1972) suggested that many species had cosmopolitan abyssal distributions. This study suggests that for sites separated by 2500 km in the central Pacific, similarity levels may still be as high as 74% (Table 6.5). The important point is that these similarity levels are extremely sensitive to sampling intensity – increase sampling intensity and the similarity increases (Figure 6.22). Hence for extremely *undersampled* sites to have similarity levels over 70% is indicative that there is very little variation in community composition at these spatial scales. The real similarity levels may in fact be much higher. In other words, the evidence suggests that the entire equatorial Pacific region is a single homogenous province.

Grassle and Maciolek (1992) estimated that for every km, a single new species is generated. Given this, it could be hypothesised that the differences in species composition between ECHO 1 and DOMES A should be large, as 2500 new species would have appeared in the distance between the two sites. 2500 new and different species at ECHO 1 compared to DOMES A would, if this were the case, contribute to a low level of similarity. But this is not borne out in the analysis. Similarly, at a functional and family taxon level, all the abyssal Pacific sites, if not all the abyssal sites globally are virtually identical. The differences in species composition between the Atlantic and Pacific sites are unknown; in this modern world of molecular genetics it would be unwise to suggest that morphologically similar species, separated by such distances, are in fact the same species. But personal observation of both Atlantic and Pacific faunas hints that for many of the more abundant species, few morphological differences can be ascertained. This observation is supported by the work of Kirkegaard (1994) and Levenstein (1972) who were working on larger polychaetes for which a more complete taxonomic database was available. For small infaunal polychaetes, more taxonomic work is needed to confirm potential cosmopolitan distributions.

These observations of both alpha and beta diversity do not lend the author to think that species diversity in the abyss is particularly high on a regional scale. This may be more of a personal observation than qualified fact at present. Certainly, at a local level, an exceptionally large number of species co-exist in a few square meters of sediment. But at a regional scale, diversity may not be anywhere near reaching the levels seen in tropical terrestrial systems. The observations of Grassle and Maciolek (1992) were made on the continental slope, which may exhibit higher levels of beta diversity than in the abyss. The two most distant stations in that analysis were separated by only 176 km, and showed similarity levels of 79% for 50 individuals. This can be compared to a 74% level of similarity at 2500 km in this analysis, supporting the idea that beta diversity may be higher in shelf sediments. Some caveats must be admitted in the use of similarity indices. The 74% level is based on a NESS analysis for 10 individuals. When more than 10 individuals are used, NESS can be expected to decrease. However, the similarity between DOMES A and the other manganese nodule sites, separated by 2000+ km, is still 67% when a NESS at 60 individuals is used, and 56% when 200 individuals are sampled. Were sampling to be increased, the similarity levels would almost certainly be significantly increased. In summary, there is no evidence to support the hypothesis of high abyssal beta diversity at this stage – so, in keeping with the data, the hypothesis is not erected.

May's (1992) argument against the high regional deep-sea diversity postulated by Grassle and Maciolek (1992) was that species replacement with distance is unlikely to be linear. This study supports this argument, at least for abyssal polychaetes. There is no evidence of decreasing similarity with distance (Figure 6.22). There is evidence of increasing similarity with sampling intensity.

Quantifying beta diversity is crucial to these estimates of total species richness. There is no evidence from this study that species replacement in the abyss is as high as that discovered on continental shelf slope depths. It is not possible to generate a precise estimate, but the total number of polychaete species in the abyssal Pacific is likely to be in the thousands rather than the millions. Polychaetes generally account for around 50-60% of the macrofaunal organisms in bathyal and abyssal habitats, hence this finding is likely to be of considerable consequence to estimates of global species richness.

7.4 Future Directions in Abyssal Ecology

> *"The longer you are in the presence of a difficulty, the less likely you are to solve it."*
>
> *- Charles Nicolle*

Nicolle was referring to the problem of conditioned thinking, a natural tendency to persevere with a line of inquiry while the real explanation lies on a different path. No scientist can be free from conditioned thinking; all learning is a conditioning of the mind. But some steps can be taken to minimise its unwanted side-effects. These steps are backward ones – a 'back to basics' approach. In ecology, this approach might ask – why does a species live in a particular habitat? The answer is, because it evolved, it could get there and local processes allow it to persist. Figure 7.4 illustrates the general theory of this approach, the central theme of this chapter.

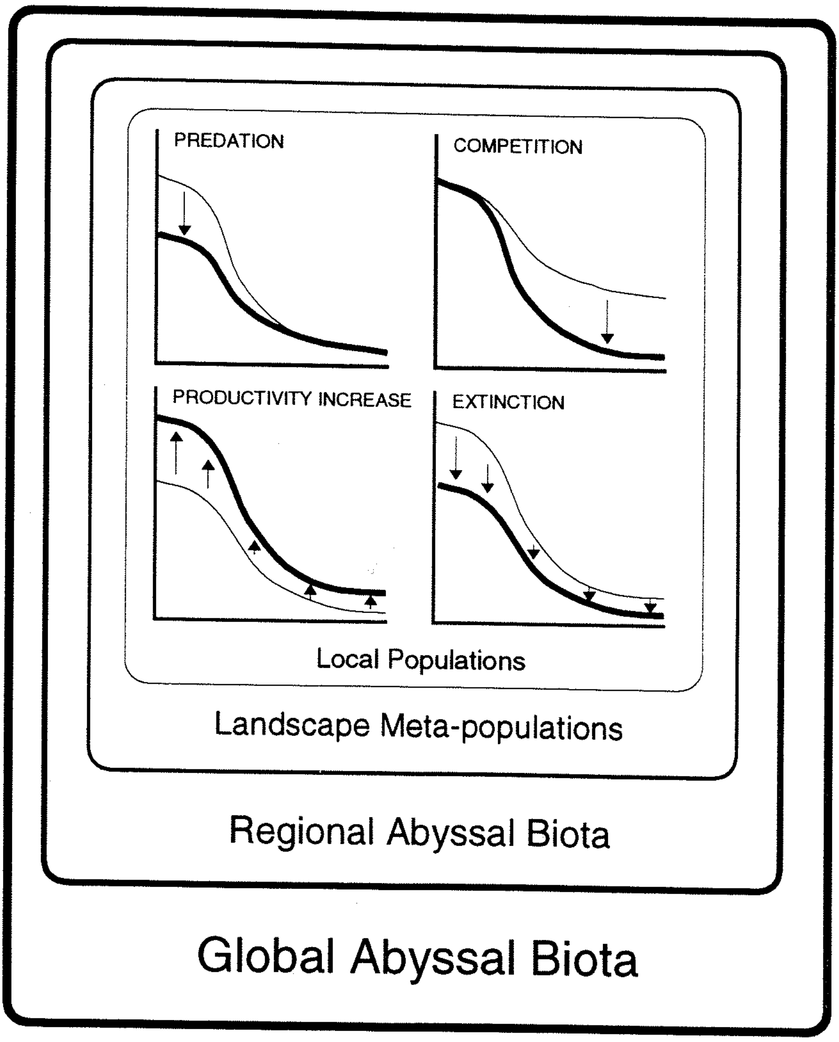


Figure 7.4 Local species abundance patterns (graphs indicate species abundance in rank order) operate within the general framework of landscape meta-populations, regional biotas (the regional enrichment model) and global biotas (evolution and speciation).

At the start of this chapter, the suggestions of Ricklefs and Schluter (1993) were outlined and their general applicability to deep-sea ecology questioned. It is of use to review these ideas with regard to the general observations put forward in this thesis. Further studies that would enhance knowledge of deep-sea ecology are suggested.

1. Characterising scales of diversity in the deep sea

Ricklefs and Schluter (1993) called for *"...systematic comparisons of diversity between continents or ocean basins within carefully matched habitats and with multiscale sampling in order to assess regional and local components of diversity."* This study has indicated the importance of isolating diversity at the alpha and beta scales, even if they may be somewhat artificial constructs. In the abyss, polychaete alpha diversity is high, but the evidence does not suggest that beta diversity is especially so, contrary to findings from continental slope depths (Grassle and Maciolek, 1992).

Future studies should focus on beta diversity, as suggested by Gray (2000). In particular, beta diversity needs to be assessed on the thousands of km scale before any generalisations regarding regional diversity and total global species richness can be made. Labour intensive quantitative box core sampling programmes may not be required for such an investigation; single large samples taken using epibenthic sleds, screened using the same procedures as box cores, may provide a more cost-efficient method of appraising such biogeographical patterns. The small size of the box core relative to sledges and trawls results in very low sample sizes in oligotrophic sites such as the HOT station. The use of larger sampling devices in these areas may help to redress this balance, although it may not be appropriate to compare faunas taken using different sampling methodologies, as indicated in the analysis of family composition from the HMS *Challenger* material (Chapter 6).

2. Relationship between scales of diversity in the deep sea

Evaluating the dependence of local diversity on regional diversity is an important step towards a broader theoretical understanding of species diversity patterns. The results from this study, and that of Stuart and Rex (1994) hint that deep-sea species assemblages may be unsaturated, and hence cannot be explained in a locally deterministic way. It may not be possible to separate local ecological processes from a broader regional-historical perspective.

Evidence for this hypothesis will be founded in better studies of regional diversity patterns, as suggested above. Additionally, the regional enrichment model hints that source-sink effects may play a significant role in deep-sea ecology (Pulliam, 1988). Locally abundant and species rich areas, such as the EqPac upwelling zone and the north-east Atlantic may provide a source for recruitment to the vast oligotrophic gyre regions of the worlds oceans. The testable hypotheses of this theory are (1) that many deep-sea polychaetes exhibit planktotrophic modes of dispersal, and are widely distributed, (2) that many polychaetes at oligotrophic sites do not reach reproductive maturity. Further work on the reproductive biology of individual species is required to evaluate this idea, with potential effects on much larger scale ecological patterns.

3. The intrinsic properties of the deep-sea habitat, and their relationship with regional diversity patterns

Ricklefs and Schluter (1993) suggested that *"...ecologists must take a more active role in investigating the processes of species production and extinction"*. This study has provided intriguing evidence that large-scale natural physical disturbances may impact deep-sea communities on a spatial scale of thousands of km. A spatio-temporal continuum of disturbances, from small-scale bioturbation effects with ecological significance, to the abyssal extinction events of the late Mesozoic could be the setting for the generation and maintenance of deep-sea diversity. The results from the Madeira Abyssal Plain hint that at certain spatio-temporal scales, ecological and evolutionary processes may overlap.

This junction of geological history and local ecology may provide the framework for speciation in an otherwise monotonous habitat. Further work in this area should focus on the spatial scale of turbidite disturbances and their temporal mode. Polychaetes do not preserve well in the fossil record, but other taxa do, and their geological history may shed light on the influence of turbidites on both a local and regional level.

4. Systematic and evolutionary history of deep-sea species assemblages.

To understand the regional-historical influences on local species diversity requires knowledge of the phylogenetic history of species assemblages. There have been several studies of the phylogenetic patterns of deep-sea crustaceans, in particular the very diverse deep-sea group, the isopods (Hessler and Wilson, 1983; Wilson, 1999). Future combined morphological and molecular approaches in deep-sea taxonomy would illuminate further the historical contingency on deep-sea diversity. There has been little work on the evolutionary diversification of Polychaeta in the deep-sea, which may turn out to be their most abundant and species-rich habitat. Recent extensive phylogenies of deep-sea polychaetes, both at a morphological (Rouse and Fauchald, 1997) and molecular (Brown *et al.*, 1999) level should be used as a starting position with which to investigate phylogenetic constraints in the deep-sea.

Certain areas of the deep ocean may act as centres of diversification and speciation. The recent studies of the genetic diversity of *Deminucula atacellana* have shown how bathyal regions are hotspots of speciation, from which abyssal invasions probably took place (Etter and Grassle, 1992). Molecular approaches may provide the tools for a more complete understanding of adaptive radiation into the deep sea. For polychaetes, where morphological variation is reduced, or at least less well documented, molecular methods will provide a more robust route to answering these questions.

Many future discoveries await the fusion of ecological and evolutionary studies of deep-sea diversity. On a short-term ecological scale, new advances in biogeochemistry combined with high quality time-series data sets will further understanding of functional deep-sea ecology. On a longer-term macroecological scale, a combined systematic and ecological understanding may yet make for an exciting scientific synthesis.

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9 APPENDIX ONE: RAW DATA ON CD-ROM

In *Microsoft Excel 97 for Windows* format.

The CD-ROM is in a sleeve in the inside cover of bound copies of this thesis.

10 APPENDIX TWO: RESEARCH PAPERS IN PRESS

The following manuscripts of scientific papers stem in part from research conducted for this PhD and are all either published or in press at the time of final submission.

Glover, A.G., Paterson, G.L.J., Bett, B., Gage, J., Sibuet, M., Sheader, M. and Hawkins, L. (2001) Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, north-east Atlantic. *Deep-Sea Research I* **48**, 217-236.

Paterson, G.L.J. and Glover, A.G. (in press) A new species of *Sigambra* (Polychaeta: Pilargidae) from the abyssal plains of the NE Atlantic. *Bulletin of the Natural History Museum (Zoology Series)*

Lambshead, P.J.D., Tietjen, J., Glover, A.G., Ferrero, T., Thistle, D. and Gooday, A. (in press) The impact of large-scale natural physical disturbance on the diversity of deep-sea north Atlantic nematodes. *Marine Ecology Progress Series*

Reprints from these publications are reproduced on the following pages.

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DEEP-SEA RESEARCH
PART I

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Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic

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Abstract

Polychaete abundance and diversity patterns from the Madeira Abyssal Plain (MAP) were studied together with data from three other sites on the northeastern Atlantic abyssal plains. Polychaete abundance at MAP was significantly lower than at any of the other sites, including those lying under comparable productivity regimes. Analysis of diversity, using rarefaction and species counts per unit area, suggests that MAP is extremely species poor and shows dominance by a few common species. The MAP site is characterised by a superficial layer of turbidite sediment, and the hypothesis is put forward that the unusual sediment characteristics at MAP have affected macrofaunal abundance over a vast area (>2000 km^2). Analysis of species composition indicates that the MAP site is not faunistically unique; rather it contains a high proportion of widespread, abundant, cosmopolitan species. We suggest that these are the opportunists of the abyssal benthic habitat. Differences in abundance between the other abyssal sites are the result of both productivity and local environmental conditions. Equitability at the other north Atlantic sites is not affected by productivity, although the actual number of species per unit area is affected, showing a south–north gradient. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Deep sea; Polychaeta; Productivity; Turbidite; Biodiversity; Biogeography; Northeast Atlantic; Madeira Abyssal Plain

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1. Introduction

Four abyssal sites in the north Atlantic provided the focus for a large-scale European Union Marine Science and Technology (MAST II) funded project (Rice et al., 1995). The sites were originally chosen to investigate the effects of productivity and seasonality on the abyssal benthos, being sited on a latitudinal gradient from 49°N to 20°N. The project also allowed for a taxonomic analysis of the dominant infaunal organisms. In this paper, new data from the Madeira Abyssal Plain (MAP) are analysed in conjunction with polychaete data already gathered from the Porcupine Abyssal Plain (PAP), the Tagus Abyssal Plain (TAP) and the Cape Verde Abyssal Plain (EUMELI oligotrophic site, EOS) (Sibuet et al., 1993; Rice et al., 1994; Gage et al., 1995; Lambshead et al., 1995; Paterson et al., 1998).

Deep-sea sampling efforts over the last 30 yr have indicated that the abyssal habitat, while food impoverished and low in standing stock, is highly species rich (Hessler and Sanders, 1967; Hessler and Jumars, 1974; Grassle and Maciolek, 1992; Gage, 1996; Paterson et al., 1998). Resource availability for the benthos is a very important factor and has been shown to vary over both temporal and spatial scales (Deuser and Ross, 1980; Billet et al., 1983; Smith et al., 1992, 1997). In particular, a number of studies have indicated that food input in the form of particulate organic carbon (POC) flux may increase faunal abundance on the deep-sea floor (Richardson and Young, 1987; Sibuet et al., 1989; Thurston et al., 1994; Smith et al., 1997). Longhurst et al. (1995) have categorised surface biogeochemical provinces based on satellite measured chlorophyll concentrations in the euphotic zone. In this paper, we examine the relationship between these productivity estimates, midwater POC flux, and benthic abundance and diversity. Polychaetes, the dominant component of the abyssal macrofauna, form a useful assemblage with which to appraise such concepts in deep-sea ecology.

Although it is logical to suggest that benthic standing crop will be higher under areas of higher surface productivity, a number of factors may modify such a relationship. Organic matter may be degraded by microbes or utilised by midwater organisms, sources of terrestrial runoff may enhance food availability and deep sediments may be disturbed by benthic storms and turbidity currents (Gage and Tyler, 1991). During the EU MAST project it became apparent that the MAP site had been subjected to a particularly recent (1000 yr BP) turbidite event; most turbidites are associated with pre-Holocene sea-level changes (Pilkey, 1987). Sedimentation at MAP had been extensively mapped as part of an investigation into the feasibility of nuclear waste disposal in the deep sea (Roe et al., 1987). MAST cruise reports noted that there had been little pelagic sedimentation above the turbidite layers (Gooday, pers. comm.). Different sediment characteristics may also lead to a functional change in the community, so we hypothesise that the MAP site will be faunistically separate from the other Atlantic abyssal sites.

This study will also attempt to identify regional patterns of both alpha and beta diversity. Rex et al. (1993) and Rex (1997) have suggested that a latitudinal gradient of deep-sea macrofaunal diversity exists for isopods, gastropods and bivalves in the north Atlantic, with greatest diversity in the low latitudes, although Lambshead et al. (2000) suggested that for a meiofaunal phylum, nematodes, the opposite is true and that diversity reflects the productivity patterns of the north Atlantic. The present study will examine the hypothesis that the alpha diversity of polychaetes will follow the meiofaunal rather than the macrofaunal pattern of latitudinal variation while beta diversity will be assessed in the light of the suggestion by Paterson et al. (1998) that there is high species turnover in deep-sea polychaetes.

2. Methods

2.1. Localities

Table 1 summarises the known physical and biological properties of the sites. The MAP study site lies at 31°N 21°W in 4900 m of water. In the mid-1980s, a major geological survey of the Great Meteor East Site (GME), 4°W of the MAP site, was undertaken as part of an investigation into the feasibility of high-level radioactive waste disposal in the deep sea (Nuclear Energy Agency, 1984). As a result, this area is probably the most extensively surveyed region of abyssal plain in the world (Weaver et al., 1987). In fact, the true abyssal plain (at GME) lies at a depth of 5400 m; the MAP site actually lies on the lower rise on the path of turbidite flow (Fig. 1). Sediments in this area fall into two types – turbidites and pelagic sediments. Weaver and Rothwell (1987) made extensive maps of all the turbidites and concluded that the majority of them were formed by sea-level changes during interglacial–glacial transitions. However, the most recent turbidite (a), has been dated to just 930 yr BP (Thomson and Weaver, 1994) and appears to cover most of the MAP area to a depth of at least 90 cm. The extremely low sedimentation rates of 1–10 mm kyr^{-1} (Weaver and Rothwell, 1987) have resulted in only a thin veneer of pelagic sediments lying above turbidite (a).

Huggett (1987) describes the turbidite and pelagic sediments at GME as varying in two important factors — shear strength and organic carbon content. Turbidite sediments are more cohesive with a shear strength of 2–3 kPa, whereas pelagic sediments have values of only 0.3–0.6 kPa. Compaction, changes in sediment water content, decreased bioturbation and spatial or temporal changes in grain size composition could influence shear strength. Organic carbon content in the surface layers of the pelagic sediments is 0.12–0.15% and twice this in the turbidite sediments. Colley and Thomson (1985) found up to 1.75% organic carbon at 50 cm depth in some of the turbidite cores. In a separate study of multi-cores from the MAP site, Wolff et al. (1995) found that normally labile lipids are present in high concentrations throughout the turbidite and that this was closely correlated with nematode abundances. However, organic carbon content was not significantly higher than that in pelagic sediments (in contrast to the results from GME). Undisturbed multi-cores taken from the area showed little evidence of any pelagic sedimentation above the turbidite layer. They concluded "that the sedimentary geochemistry appears to have been strongly influenced by the recent ... deposition of a turbidite". Bottom photographs at MAP show no evidence of a seasonal phytodetritus fall (Rice et al., 1994; Thurston et al., 1998).

Three other sites in the north Atlantic were also studied as part of the MAST programme. Physical and biological characteristics of these sites are provided in Table 1. The southernmost site, on the edge of the Cape Verde Rise–Abyssal Plain, is the French EUMELI oligotrophic site (EOS); the details of this site are given in Sibuet et al. (1993) and Cosson-Sarradin et al. (1998). Details of the sampling programme for the TAP site are given in Gage et al. (1995). The PAP site is described in studies associated with the IOSDL DEEPSEAS programme (Rice et al., 1994; Thurston et al., 1994).

Table 1

Physical and biogeochemical characteristics of the four abyssal sites

	PAP	TAP	MAP	EOS
Position (centred on)	48°N 16°W	38°N 11°W	31°N 21°W	20°N 30°W
Depth (m)	4800	5035	4900	4600
No. of samples	5	6	5	8
Sampling method	Spade Box Core 0.25 m^2	Vegematic SBC 0.09 m^2	Spade Box Core 0.25 m^2	Spade Box Core 0.25 m^2
Surface productivity regime[a]	240	122	122	106
Seasonality	Seasonal Spring Bloom[b]	Not seasonal	Not seasonal	Not seasonal
Sediment type	Pelagic	Pelagic	Turbidite	Pelagic
Current speed	Low	Low	Low (7.5 cm s^{-1})	Low (3 cm s^{-1})
POC flux (g C m^{-2} yr^{-1})	0.8[c] 1.0[f]	n/a	0.41–0.57[d]	0.3[e] 0.36[g]
Sedimentation rate (cm k yr^{-1})	3[h]	n/a	0.1–1[i]	0.5[j]
C/N ratio	4.8–7.8[h]	n/a	6–9[k]	n/a
Megafaunal abundance (no. ha^{-1})	73[l]	n/a	22 (GME site[l])	10[l]
Megafuanal biomass (g ha^{-1})	1974[l]	n/a	113 (GME site[l])	63[l]
	Holothurians dominant		Asteroidea, Decapoda dominant	Decapoda dominant traces
Polychaete abundance (ind m^{-2})	342 (this study)	258 (this study)	70 (this study)	143 (this study)
Nematode abundance (ind 10 cm^{-2})	388[m]	n/a	80[m]	72[m]

[a] Longhurst et al. (1995).

[b] Rice et al. (1994).

[c] Newton et al. (1994).

[d] Lampitt (1992).

[e] Heuser and Khripounoff (1993).

[f] Honjo and Manganini (1993).

[g] Rabouille et al. (1993).

[h] Santos et al. (1994).

[i] Weaver and Rothwell (1987).

[j] Auffret et al. (1992).

[k] Wolff et al. (1995).

[l] Thurston et al. (1998).

[m] Lambshead et al. (1995).

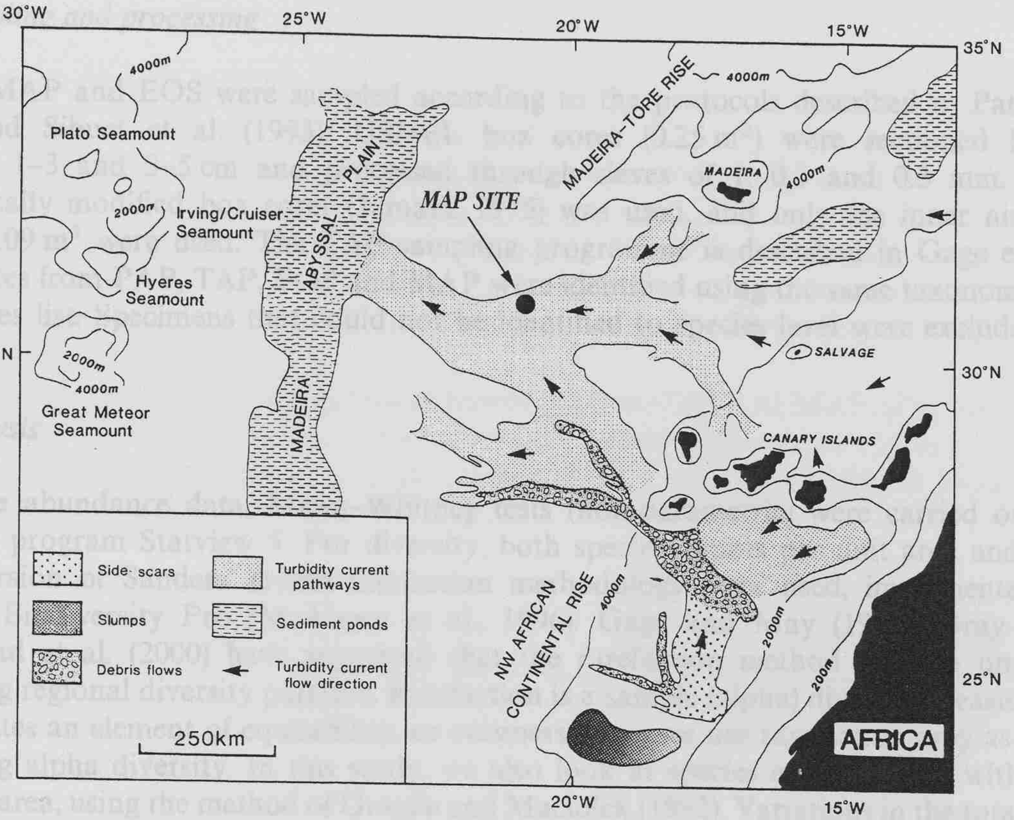


Fig. 1. Map of the MAP region. Tracks of the various turbidite events are shown (after de Lange et al., 1987).

Longhurst et al. (1995) have categorised oceanic biogeochemical provinces using data from the Coastal Zone Colour Scanner (CZCS) carried aboard the NASA Nimbus-7 satellite. Details are provided in Table 1. In a review of POC flux data, Lampitt and Antia (1997) have shown that increasing productivity from 100 to 200 g C m^{-2} yr^{-1} leads to an increase in POC flux, but when surface productivity rises above 200 g C m^{-2} yr^{-1}, flux does not increase beyond 3.5 g C m^{-2} yr^{-1}. POC flux data for the four sites are provided in Table 1. POC flux and sedimentation rates at MAP are extremely low, comparable with those at the oligotrophic EOS station. At PAP, flux is also low considering the levels of surface productivity, although the sedimentation rate reported by Santos et al. (1994) is much higher than at the oligotrophic sites.

In summary, two important variables are likely to be impacting the benthos at these four sites. At MAP the sediments are composed of turbidite deposits different in character from the pelagic sediments at the other three sites. At PAP, POC flux to the sediment is enhanced compared to the other three sites. TAP and EOS, both seemingly unaffected by recent turbidites or enhanced POC flux can be used as controls with which to compare the turbidite-affected MAP and POC flux-enhanced PAP sites.

2.2. Sampling and processing

PAP, MAP and EOS were sampled according to the protocols described in Paterson et al. (1994) and Sibuet et al. (1993). USNEL box cores ($0.25\,m^2$) were sectioned horizontally into 0–1, 1–3 and 3–5 cm and processed through sieves of 1, 0.5 and 0.3 mm. At TAP a vegematically modified box corer (Jumars, 1975) was used, and only the inner nine subcores of area $0.09\,m^2$ were used. The TAP sampling programme is described in Gage et al. (1995). Polychaetes from PAP, TAP, EOS and MAP were identified using the same taxonomic database and species list. Specimens that could not be identified to species level were excluded from the analysis.

2.3. Analysis

For the abundance data, Mann–Whitney tests (non-parametric) were carried out with the computer program Statview 5. For diversity, both species counts per unit area and Hurlbert's (1971) version of Sanders' (1968) rarefaction methodology were used, implemented with the program Biodiversity Pro (McAleece et al., 1996). Gage and May (1993), Gray (1997) and Lambshead et al. (2000) have suggested that the rarefaction method may be unsuitable for comparing regional diversity patterns. Rarefaction is a sample (alpha) diversity measurement that incorporates an element of equitability, or evenness. Here we use rarefaction only as a means of comparing alpha diversity. In this study, we also look at species accumulation with increasing sampling area, using the method of Grassle and Maciolek (1992). Variations in the total number of species per unit area may be a function of both the amount of food available and the regional–historical pool of species. A comparison of $E(S_n)$ with species per unit area provides a clue to the relative importance of local and regional processes in structuring the "total" biodiversity of the deep sea.

Beta diversity, or species turnover between sites, was estimated with a Kulczynski (1927) similarity index based on the pooled data. This simple index calculates a percentage similarity based on the number of both shared and unique species in a site. Analysis of the biogeographic relationship between the sites was carried out by the ecological cladistic methods of Lambshead and Paterson (1986), implemented with the programs PAUP 3.1.1 (Swofford, 1993) and MacClade 3.0.7 (Maddison and Maddison, 1992). This method uses the traditional phylogenetic "maximum parsimony" approach to group sites (rather than species) based on shared species (rather than characters). The Camin-Sokal algorithm in PAUP was enabled, so that only species presences are used to classify sites, not species absences (which may occur due to sampling inefficiency). Tree "branch lengths" were calculated with PAUP and represented graphically on the final tree. Species were categorised into four groups. *Cosmopolitan* species recorded from all sites; *3-site cosmopolitan* absent at only one site; *widespreads* recorded from sites on different branches or geographic clades; *regional species* found at two sites linked in the same geographic clade and finally *endemic/unique* species at one particular site only. The percentage of individuals contributing to each group was then calculated. A visual comparison of the importance of each group in each site was then possible by plotting the data as a stacked column chart. Examining this in conjunction with the tree classification is a simple and effective way of studying the importance of the numerically dominant species in the system.

3. Results

3.1. Abundance

Polychaete abundance at MAP was significantly lower ($p < 0.05$) than at the other MAST sites (Table 2; Fig. 2). There was a mean abundance of 70 ind. m^{-2} at MAP, while the other tropical Atlantic site EOS had a mean abundance of 143 ind. m^{-2}. Polychaete abundances at PAP and TAP were 342 and 258 ind. m^{-2}, respectively, both significantly higher than at EOS. The lower values in polychaete abundance described in this study compared with Paterson et al. (1998) are due to reassessment of the data.

Polychaete abundance is plotted against sediment depth in Fig. 3. At MAP, although generally low in abundance, polychaetes were distributed more evenly throughout the sediment layers, identical to the pattern of vertical distribution found at PAP. Polychaetes at EOS are very superficially distributed within the 0–1 cm layer.

Table 2
Comparison of polychaete abundance (m^{-2})

	Abundance (mean)	S.D.	TAP	MAP	EOS
PAP	342	81	NS[a]	[b]	[b]
TAP	258	103		[b]	[b]
MAP	70	31			[b]
EOS	143	40			

[a] NS = not significant.
[b] Significance at $P < 0.05$ level (Mann–Whitney).

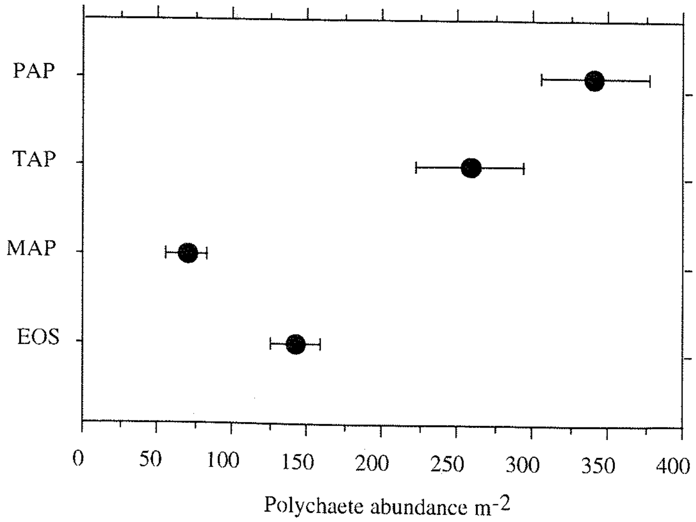


Fig. 2. Polychaete abundance in the abyssal northeast Atlantic. With the exception of PAP and TAP all sites are significantly different from each other (Mann–Whitney, $p < 0.05$). Error bars are ± 1 standard error.

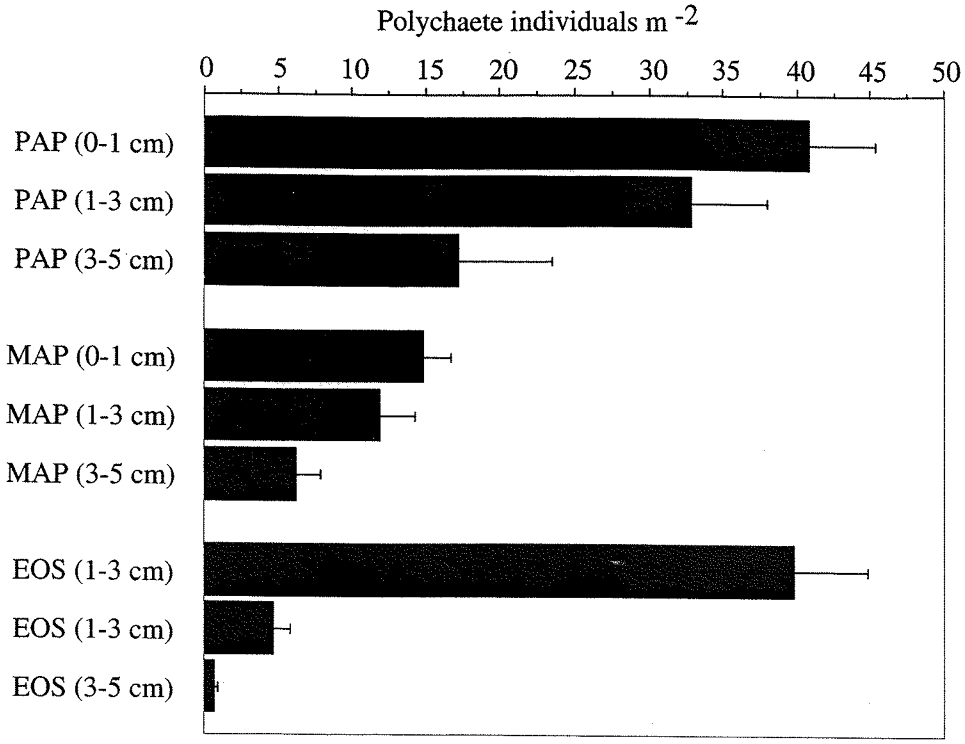


Fig. 3. Polychaete abundance split by sediment depth layer. Error bars are ± 1 standard error.

Table 3
Analysis of familial composition (%)

MAP		PAP		TAP		EOS	
Spionidae	22	Spionidae	27	Cirratulidae	17	Cirratulidae	31
Cirratulidae	19	Cirratulidae	26	Opheliidae	15	Spionidae	16
Paraonidae	18	Paraonidae	11	Spionidae	15	Paraonidae	11
Ampharetidae	8	Sabellidae	6	Paraonidae	13	Sabellidae	7
Pilargidae	7	Pilargidae	4	Pilargidae	11	Flabelligeridae	9
Other	26	Other	26	Other	29	Other	26

3.2. *Taxonomic composition*

A total of 29 species were recorded from MAP, compared to 101 at PAP, 57 at TAP and 75 at EOS. An analysis of familial composition (Table 3) indicates that the sites are functionally very similar, with cirratulids, spionids and paraonids, all deposit-feeding polychaetes, present in the top five families. A predatory pilargid, *Sigambra* sp., was abundant at PAP, TAP and MAP but rare at EOS. Opheliids were one of the dominant five families at TAP but not at the other sites.

3.3. Species diversity

MAP was lowest in diversity both in terms of species counts per unit area (Fig. 4A) and $E(S_n)$ (Fig. 4B). There were fewer polychaetes, fewer species of polychaete and greater dominance of particular species (in this case *Prionospio* sp., *Chaetozone* sp., *Aricidea* sp. and *Sigambra* sp.) at MAP. At the other MAST sites, local diversity was similar with rarefaction curves not significantly different from each other (Mann–Whitney, $p < 0.05$). The sites have similar $E(S_{80})$ values of approximately 40; only the MAP site is lower.

The number of species per unit area is lower at MAP than at the other sites (Fig. 4A), with the number of species increasing only gradually as samples are accumulated. Of the other sites, PAP has the highest number of species per unit area, followed by TAP and then EOS.

3.4. Regional patterns in species composition

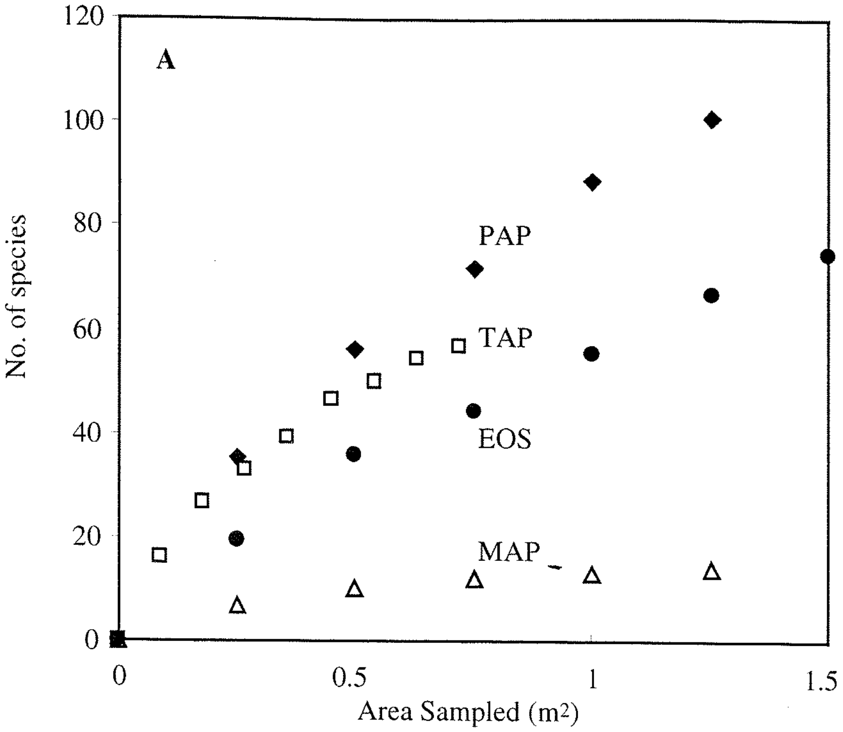
Kulczynski analysis indicates that all MAST sites have very low similarity levels. MAP groups mostly closely with EOS, but the similarity is only 26%. PAP and TAP group together with a similarity of 26%. Only five species were present at all four sites, and only 11 species at at least three sites. 67 species were unique to PAP, 33 to TAP, 20 to MAP and 52 to EOS. 81% of all species found were unique to particular sites.

The ecocladistic analysis generated a single most parsimonious tree (Fig. 5), with the two northern sites (PAP and TAP) clustering separately from the two southern sites (MAP and EOS). The strength of these geographic clades can be assessed by plotting branch lengths using PAUP. Branch lengths of the individual sites are extremely long, indicating a high number of unique species, whereas the branch lengths of the nodes are extremely short, indicating that the geographic clusters are not well supported. The significance of the geographical clusters was assessed by calculating the numerical abundance of the different species categories (Fig. 6). Although the great majority of species were unique, the great preponderance of individuals belonged to cosmopolitans and widespread species. At MAP, approximately 70% of individuals were cosmopolitans or widespread, with unique and regional species contributing a much smaller proportion of the fauna. At PAP and TAP approximately 50% of the population belonged to cosmopolitan/widespread species, while at EOS this proportion was just over 30%.

4. Discussion

4.1. Patterns of polychaete abundance in the northeast Atlantic abyss

The most surprising result of this study are the extremely low polychaete and macrofaunal abundances at MAP. Abundance is less than half that at the more oligotrophic site at EOS. Neither megafauna (Thurston et al., 1994) nor nematodes (Lambshead et al., 1995) show this pattern (Fig. 7). Megafaunal data also indicated that, in addition to decreasing numbers, there were taxonomic differences (Thurston et al., 1994): a nearly complete absence of holothurians at MAP, with Asteroidea and Decapoda the dominant component. Sibuet et al. (1993) showed that megafaunal abundance was also very low (in comparison with PAP) at EOS, so it may well be that


A
120
100
80
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40
20
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No. of species
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TAP
EOS
MAP
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1
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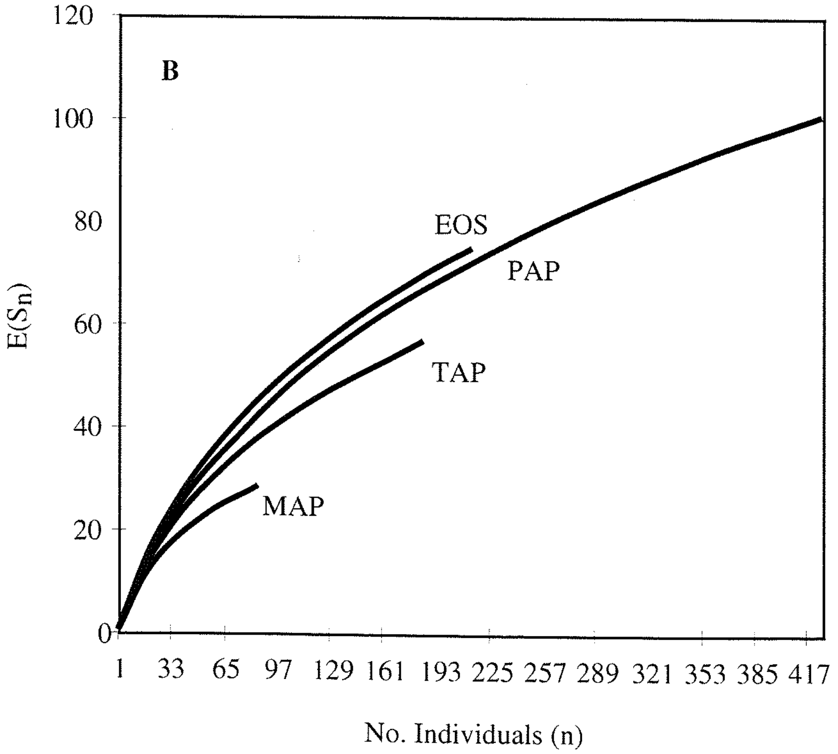
Area Sampled (m2)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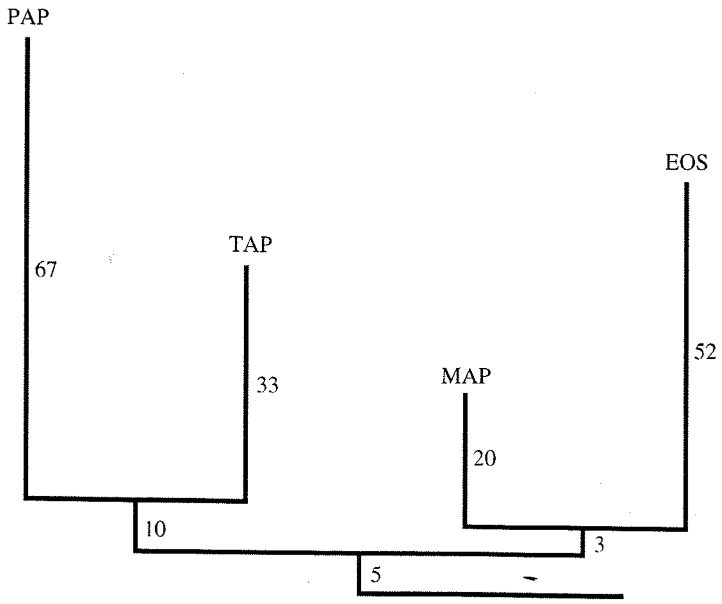

Fig. 5. Ecocladistic dendrogram showing the relationship of the sites. The numbers associated with each branch indicate the number of species which define the branch. The length of the branch also indicates the number of species which uniquely define the associated geographic clade.

MAP is not unusual in terms of megafauna. It is difficult to explain the low polychaete abundance at MAP. The most obvious factor might be food supply. However, Table 1 indicates that MAP has higher or at least similar levels of POC as at EOS. The only other major difference between MAP and the other MAST sites was the presence of a superficial turbidite. We discuss this further in Section 4.4.

The disparity between PAP and EOS in terms of the depth at which polychaetes are found (depth profiles) has already been noted by Paterson et al. (1998). Nevertheless, the pattern at MAP (Fig. 3) needs to be explained with reference to the hypothesis that high megafaunal activity and bioturbation at PAP enhance the depth profiles of polychaetes. It would appear from Fig. 3 that MAP does not display the same pattern as at EOS, which one might expect given the low levels of megafauna. Abundance is actually slightly higher in the 1–5 cm depth layer. The changing sediment characteristics with sediment depth may have an influence. Polychaetes may be responding to the higher levels of total organic carbon found beneath the surface layer, deposited with the turbidite.

Comparison of the MAST sites with other abyssal zone studies (Fig. 8) indicates that there is no obvious depth–abundance relationship within the abyssal zone, indicating that local conditions

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Fig. 4. Diversity of abyssal benthic polychaetes from MAST sites. (A) polychaete species accumulation curves with increasing area. At a sample of approximately 1 m^2 PAP has approximately twice the number of species as the tropical EOS and more than five times the number at MAP. (B) Rarefaction curves for the pooled data. At $E(S_{20})$ there was no significant difference in alpha diversity (equitability) between the stations, with the exception of MAP, which was significantly lower (Mann–Whitney, $p < 0.05$). Pooled $E(S_{80})$ values for the four sites are as follows: PAP, 40: TAP, 37; MAP, 28; EOS, 43. Local $E(S_{20})$ values for the sites are: PAP, 14.36; TAP, 14.68; MAP, n/a; EOS, 14.96.

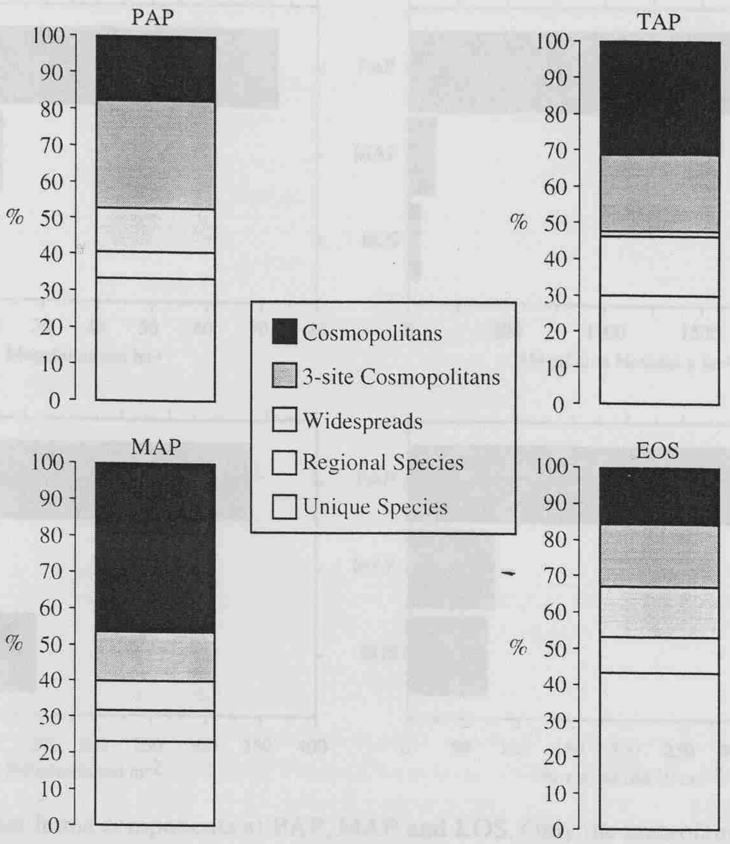

Fig. 6. Accumulative percentage histograms indicating the composition of the fauna at each site. Details of the catagories are given in the text.

vary considerably. Although there was a decline in abundance with depth, there was also considerable variation between sites within the same depth zone, concordant with the observations of Khripnouff et al. (1980). To summarise, local conditions in the Atlantic are obscuring the relationship between food supply and abundance (Rowe, 1983; Lambshead et al., 2000).

4.1.1. *Polychaete abundance as a proxy for food supply*

Paterson et al. (1998) suggested that there was a weak link between surface production and benthic standing stock. In this paper we attempted to look for a more comprehensive relationship based on all abyssal data from the North Atlantic, first using estimates of primary production from Longhurst et al. (1995) and also using particulate organic flux (POC) estimates. Lampitt and Antia (1997) suggested that at values below 200 g C m^{-2} yr^{-1} there was a good relationship between primary productivity and POC flux. If this relationship holds then it may be possible to relate abundance to primary production for those areas where there are no estimates of POC. Unfortunately, this has proved difficult.

Analysis of abundance and surface primary production estimates based on Longhurst areas failed to show any significant relationship. This result is perhaps not surprising given that the Longhurst area estimates are basin wide and do not take account of local variations, which

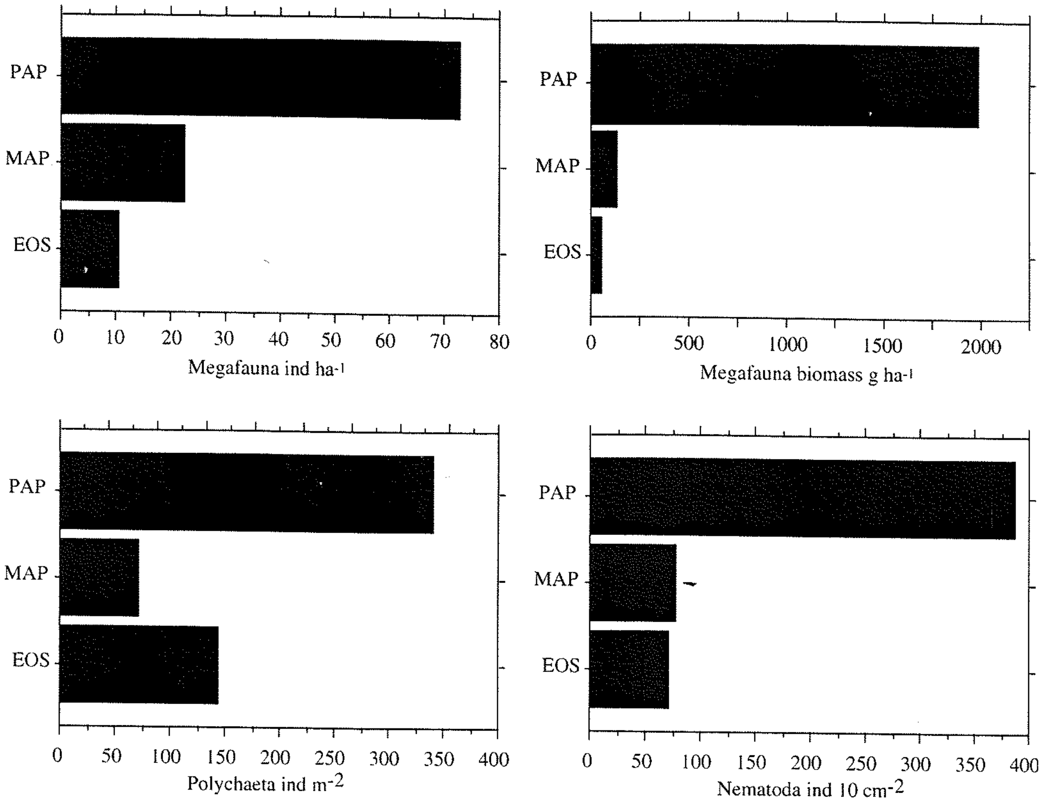

Fig. 7. Abundance of the major fauna components at PAP, MAP and EOS. Only the macrofauna showed a decrease in abundance at MAP. Nematodes and megafauna, though reduced, were more abundant at MAP than at EOS.

can be substantial. A case in point is the Caribbean Sea area overlying the Venezuela Basin, where the integrated Longhurst values estimate surface primary productivity (SPP) at 130 g C m^{-2} yr^{-1} — whereas Richardson et al. (1985), quoting Couper (1983), gave values of 54.7–182.5 g C m^{-2} yr^{-1}. By substituting (where possible) Longhurst values with locally derived estimates a better relationship can be found. This only introduces a further problem; there are fewer relevant locally derived SPP estimates, and such values can be problematic for the general user. SPP estimates are exceptionally variable and dependent on the protocol used. Without a good understanding of how the values were obtained it is possible to make erroneous comparisons (Balch, pers. comm.). Furthermore, such values may be temporally constrained and not integrated over the whole year.

Estimates of POC flux are likely to provide a better relationship with abundance (Sibuet et al., 1989; Smith et al., 1997). Here the problem arises that very few of the studies conducted in the north Atlantic have also made measurements of the POC flux; in studies where such measurements were taken no analysis of the benthos was undertaken. Such data that do exist are often temporally constrained and appear higher than expected, for example those of the Demerara Abyssal Plain (Sibuet et al., 1984). Given the effort put into studies of biogeochemical flux it is surprising and frustrating that the results are not applicable to more general studies.

Currently, our understanding of the factors affecting benthic standing crop in the Atlantic abyss is incomplete. It is clear that polychaete abundance is locally variable, affected by disturbance

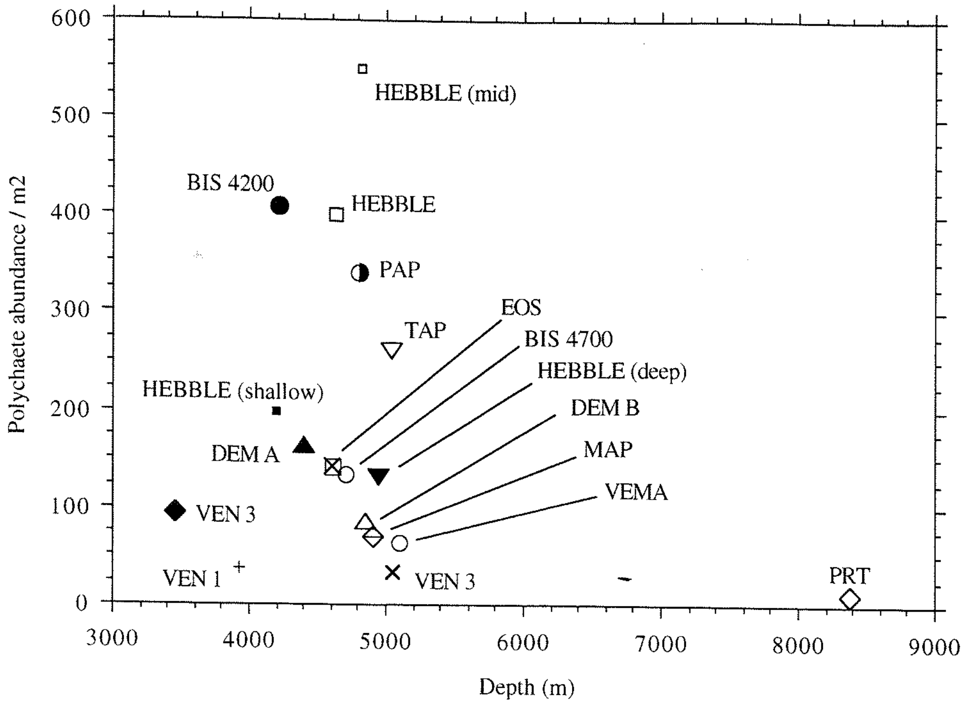

Fig. 8. Polychaete abundance (individuals m^{-2}) plotted against depth. BIS 4200 and BIS 4700 (Laubier and Sibuet, 1979); DEM A and DEM B — Demerara Abyssal Plain (Sibuet et al., 1984); HEBBLE (Thistle et al., 1985); HEBBLE — shallow, mid, deep (Aller, 1997); EOS — EUMELI oligotrophic site, MAP — Madeira Abyssal Plain, PAP — Porcupine Abyssal Plain (this study, Paterson et al., 1998); PRT — Puerto Rico Trench (Richardson et al., 1995), TAP — Tagus Abyssal Plain (Gage et al., 1995; Paterson et al., 1998), VEN 1, 2 and 3 — Venezuela Basin (Richardson et al., 1985), VEMA — Vema Fracture Zone (Khripounoff et al., 1980).

(e.g. HEBBLE) and differences in nutrient input (e.g. PAP). More general conclusions are as yet not possible. It may be that large-scale patterns will always be obscured within the Atlantic abyss because ultimately terrigenous influences are more obvious. For example, at EOS aeolian-derived silica from the Sahara Desert some 1000 km away has been detected. In the central Pacific there is a distinct relationship between productivity and abundance (Smith et al., 1997); this is a reflection of the considerable distance from any large land mass, making terrigenous influence much less likely, as suggested by Lambshead et al. (2000).

4.2. *Diversity*

MAP samples were characterised by low species diversity and higher dominance than at the other MAST sites. Such dominance is unusual in deep-sea samples, although sites such as HEBBLE with high levels of disturbance also have high sample dominance. At bathyal depths, high dominance was also noted by Paterson and Lambshead (1995) from areas swept by currents. The taxonomic composition at MAP is characterised by species with cosmopolitan or widespread distributions within the study sites in the northeast Atlantic abyss. These observations are reminiscent of a site undergoing recolonisation from disturbance. In shallow water recovery from disturbance is categorised by lower diversity, high dominance and opportunistic species with wide distributions. It is difficult to identify an obvious disturbance agent. MAP is essentially quiescent with local currents speeds below 7 cm s^{-1}. There are few major bioturbators compared with PAP (A.L. Rice, pers. comm.). We discuss in Section 4.4 the potential disturbance effect of the turbidite.

While diversity at MAP is unusually low, the other three sites show characteristic patterns of high local diversity. In this case there is no relationship between productivity and local (alpha) diversity (as measured using the rarefaction technique). Nevertheless, PAP has a much greater number of species per unit area than at EOS (Fig. 4A), a reflection of the high abundance of polychaetes at PAP. This has implications for the debate regarding the total number of species in the deep sea (see, e.g. Grassle and Maciolek, 1992; Grassle, 1992; Gage and May, 1993; Poore and Wilson, 1993). Diversity in terms of the actual number of species *will* vary over regional scales in response to changes in food input. It is not an obvious conclusion that number of species per unit area will be related to abundance. This relationship will depend on the degree of equitability in the community. The data from PAP suggest that enrichment results in an increase in the number of species and not an increase in dominance by certain specialist species. This result supports the hypothesis put forward by Lambshead et al. (2000) that polychaete diversity patterns will be similar to those for nematodes, i.e. closely related to food supply.

4.3. Biogeography and biodiversity in the northeast Atlantic abyss

It was initially thought that the MAP site would be faunistically separate from the other sites because of its unusual sedimentological characteristics, but the results from the Kulczynski analysis of faunal similarity indicate that MAP is not obviously distinct and is closest to EOS in terms of species composition. However, the similarity levels are, in general, extremely low, and it is apparent that none of the sites share very many species.

Superficially, the ecocladistic classification (Fig. 5) supports the Kulczynski result. It is apparent that individual sites are highly "derived" with unique species contributing the greatest proportion of species. Nodes are only weakly supported in terms of number of species. However, when the abundance of the different categories of species is established, a different pattern emerges (Fig. 6). A large proportion of the fauna at all the sites is composed of cosmopolitan or widespread species. This is most pronounced at MAP, which is dominated by a select group of species — these species are the cosmopolitan species of the northeast Atlantic. At the other sites, there is a greater proportion of rare and locally unique species. Such widespread distributions, crossing a number of different nutrient and sediment regimes, suggest that these species may well be opportunistic. The fauna of MAP appears to be composed of more of these potentially opportunistic species. This supports the hypothesis that the MAP site is recovering from disturbance, as discussed further in Section 4.4.

The discovery of a core group of abundant cosmopolitan species has wider implications for biogeographic and biodiversity research. There has been little or no work carried out on polychaete species distributions in the abyss, and the conservation importance of this should not be overlooked. Our data support the hypothesis that polychaetes are as widely distributed in the abyss as they are in shallow water. The large number of unique species is the result of the vast regional species pool of the deep sea and a random sub-sampling of this fauna with inadequate sampling effort. Consequently, only the abundant cosmopolitan species are found throughout; rare ones only appear as unique to each site. Faunal turnover is likely to operate over greater distances and more gradually than suggested by Paterson et al. (1998).

4.4. Has the turbidite at MAP had a lasting effect?

Richardson et al. (1995) hypothesised that the low standing crop in the Puerto Rico trench was the result of low productivity coupled with occasional turbidite disturbance. The situation at MAP is similar. The area has been subjected to a number of distinct turbidite events over the past 10,000 yr, culminating in the most recent event some 930 yr ago (Thomson and Weaver, 1994). The overlying productivity for this region is low (Roe et al., 1987; Thurston et al., 1994), and sedimentation rates are also low (Table 1). Several lines of evidence are consistent with the hypothesis of a turbidite effect. Firstly, macrofaunal abundance was very low at MAP, significantly lower than at the other MAST sites, including the equally oligotrophic EOS site. Secondly, polychaete diversity at MAP was different from that at the other abyssal sites so far examined, in that it appears to be more highly dominated. Such high dominance could be consistent with a community recovering from disturbance. Thirdly, polychaete species composition at MAP was characterised by cosmopolitan and widespread species with a lesser proportion of apparently unique species than at other sites (Fig. 8).

Against these facts must be balanced the observation that the megafauna (Thurston et al., 1994) does not show lower than expected abundance at MAP. Also polychaetes and macrofauna showed a within sediment distribution similar to that found at PAP, albeit at much reduced abundance (Fig. 3). It might be expected that the different sediment characteristics found below the first centimetre of pelagic sediment would have an effect. Finally, current understanding of recolonisation rates both in shallow water and the deep sea suggests that recolonisation can be rapid, even in areas where the disturbance has been quite large scale (e.g. the DISCOL Experiment (Borowski and Thiel, 1998)). However, Thrush et al. (1996) have suggested that large-scale disturbances can take longer to recolonise, particularly if key structuring species are removed.

The taxonomic composition of the megafauna recorded by Thurston et al. (1994) was dominated by errant species of asteroids and decapods — mostly shrimps. Such animals are relatively motile and operate on a larger scale than the small macrofauna and are likely to distribute quickly. These megafaunal species are widespread in the abyssal northeast Atlantic. The type and magnitude of the disturbance and the potential recolonisation pathways may well be significant. Large-scale disturbances in shallow water tend to be recolonised from the edges by organisms with pelagic dispersal phases (Santos and Simon, 1980; Simon and Dauer, 1976; Smith and Brumsickle, 1989).

Observations and experiments on deep-sea recovery tend to be on a small scale with the exception of the DISCOL Experiment (Borowski and Thiel, 1998) and HEBBLE study (Aller, 1997). In DISCOL, the scale of the disturbance was about 10 km^2, and it occurred only once. The disturbance took the form of ploughing up existing pelagic sediment. Recolonisation occurred on a scale of months to years. HEBBLE measured a phenomenon that occurs over a considerably larger area — hundreds to thousands of km^2. Disturbances are in the form of erosion and deposition of pelagic sediment. The frequency of the disturbance varies with the magnitude from nearly annually for large magnitude currents in excess of 25 cm s^{-1}, to every 21 d for weaker flows (Aller, 1997). Such disturbances stimulate bacterial activity that can rapidly respond to localised inputs of labile POM during and after the deposition of eroded sediment. Most of the recolonisation by polychaetes and other macrofauna may be by non-larval immigration (Aller, 1997). Even such a large-scale phenomenon appears to have a localised impact, such that not all areas are disturbed at any one time.

Both these areas differ from the conditions at MAP in one major respect — the disturbance only reworks pelagic sediment, potentially releasing nutrients or stimulating microbial activity. At MAP the disturbance removed or overlaid existing sediment with a much coarser layer of allocthonous material derived from outside the abyssal basin. If abyssal macrofauna are influenced by sediment type — as suggested by Etter and Grassle (1992) — then recolonisation is likely to have been possible only when pelagic sediment was present or by organisms with wide tolerances. The dominance of cosmopolitan species at MAP may be a reflection of this. Also the DISCOL experimental area was much smaller in extent than the area of MAP subjected to turbidite flow. The area involved at MAP is $> 2000\ \text{km}^2$. Recolonisation of such a vast region would obviously take time and would result in a different faunal community structure.

The potential of an effect on the macrofaunal community structure even so long after the disturbance event cannot be discounted. Further analysis of fauna from different areas of MAP and surrounding regions would help establish just how localised our observations are.

5. Conclusions

Our results from MAP underline the potential scale of variability between different regions of the abyss. This local variability often confounds attempts to determine large-scale patterns in the north Atlantic. While there may be latitudinal (and longitudinal) patterns of abundance and diversity linked to nutrient flux, it is clear that we lack the appropriate corroborative data.

Analysis of the distribution and abundance of species supports the hypothesis of a group of widespread dominant polychaete species in the northeast Atlantic. The regional species pool may be extensive and change only gradually over large scales in the abyss.

The data collected to date are consistent with the suggestion that the turbidite, together with low nutrient input, has affected the macrofauna at MAP. The data from Richardson et al. (1995) and this study suggest that turbidites may have far reaching effects on the fauna of ocean basin margins, abyssal regions and the hadal depths. Such is the scale of turbidite events that they could act as evolutionary forces creating geographically isolated populations and the conditions for allopatric speciation.

Further research on the genetic composition of populations of widespread species, together with analysis of their reproductive histories, would shed light on the potential speed of recovery of abyssal communities from disturbance and the degree of gene flow between widely dispersed populations.

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Impact of large-scale natural physical disturbance on the diversity of deep-sea North Atlantic nematodes

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ABSTRACT: Nematode alpha diversity from 3 physically disturbed sites in the deep North Atlantic was compared with reference sites. Nematode diversity at the HEBBLE benthic storm site was statistically, and significantly, lower than at reference sites. Nematode diversity at the Madeira Abyssal Plain site, which was subject to a turbidite dated at 930 BP, also showed a significantly lower diversity than reference sites. However, limited data suggest that diversity was not low at a Venezuela Basin turbidite site. The difference in nematode diversity between the 2 turbidite sites is ascribed to a long term change in sediment conditions at the Madeira site. The Venezuela Basin turbidite site has a sedimentation rate greater than the Maderia site by 1 to 2 orders of magnitude, and this was reflected in the sediment profiles ~~(obtained by this study)~~. Another possibility is that the Venezuela Basin turbidite is considerably older, by at least 1000 yr, than the Madeira turbidite, allowing more time for recolonisation. The data suggest that deep-sea nematode diversity may be affected by physical disturbance but that deep-sea nematodes, like their shallow counterparts, are more robust than macrofauna such as polychaetes to such impacts.

KEY WORDS: Physical Disturbance · Deep Sea · North Atlantic · Nematodes

INTRODUCTION

The last 3 decades of the 20th century have seen a substantial increase in the number of investigations that involve analysis of the biodiversity of deep-sea nematodes, particularly in the North Atlantic. This accumulation of results from individual projects over 3 decades has presented an opportunity to study deep-sea nematode biodiversity over large distances. Prior to 1980, little was known about the diversity distributions of deep-sea nematodes over larger scales, let alone the processes underlying such patterns. Deep-sea nematology has had a slow inception because (1) the limited numbers of marine nematologists have, understandably, tended to focus on shallow waters where experimentation is possible, (2) quantative sampling was not possible until the development of the spade-box corer and, especially, the Barnett multicorer, and (3) the primitive state of deep-sea nematode taxonomy makes biodiversity analysis of samples difficult and laborious. Deep-sea nematode research is still in the stage of identifying statistically significant patterns and inductively associating these with ecological, biogeographical and historical properties of the environment to develop hypotheses of the mechanisms that control biodiversity. Developing technologies to test these hypotheses will be expensive and time consum-

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ing. It is, therefore, important to extract as much information from pattern analyses of current data as possible to synthesise hypotheses that will be productive for further testing, given the limited resources available.

Using an accumulated deep-sea nematode database, Boucher & Lambshead (1995) investigated the relationship between nematode diversity and depth, and Lambshead et al. (2000) analysed latitudinal diversity gradients in the deep North Atlantic Ocean. Both studies concluded that productivity was an important factor in producing nematode biodiversity and species richness patterns, respectively, over large distances.

Current ecological theory suggests that both productivity and disturbance influence biodiversity patterns over ecological time scales (Huston 1994). Experimentation on shallow-water nematodes has suggested that both physically (Schratzberger & Warwick 1998) and biologically generated disturbance (Austen et al. 1998) can cause modest changes in nematode diversity. The impact of physical disturbance on deep-sea nematodes has been investigated only to a limited degree and the effect of biological disturbance has not been investigated at all. Lambshead et al. (1994) compared the diversity of bathyal nematodes in the Rockall Trough with the San Diego Trough. San Diego Trough is a physically undisturbed area whereas Rockall Trough has sufficient moderate physical disturbance in the form of water currents sufficient to ripple the sediment and affect polychaete diversity (Paterson & Lambshead 1995). Lambshead et al. (1994) could find no evidence that nematode diversity, unlike polychaetes, was influenced by moderate water current disturbance. Nevertheless, Boucher & Lambshead (1995) hypothesised that low diversity in estuarine and hadal nematode communities was partly a result of physical disturbance. Glover et al. (~~■in press~~ 2001) reported that large-scale physical disturbance had long lasting influences on deep-sea polychaete diversity. Lambshead et al. (2000) suggested that there was some evidence for reduced nematode diversity in deep-sea sites affected by large-scale physical disturbance with a higher impact than the energy currents found in the Rockall Trough.

This paper will analyse the available data to determine (1) whether the available abyssal nematode biodiversity data show evidence of the effects of large-scale physical disturbance, and (2) whether analysis of a turbidite site can give some time frame for recovery from disturbance. To achieve this, it will use a database sourced from 4 research programmes that identified more than 7000 deep-sea nematodes in 43 samples from 9 locations.

METHODS

Sites. The sites utilised for this study have been described in a number of publications that are listed below; accordingly, only brief descriptions will be given here. The data sets were the same as those used by Boucher & Lambshead (1995) and Lambshead et al. (2000), see Table 1 and references for full description of sites. The reference sites include the Porcupine Abyssal Plain (PAP, Rice & Lambshead 1994, Thistle et al. 1995), the Hatteras Abyssal Plain (HAP, Tietjen 1989) and the Venezuela Basin Stns 1 & 3 (VB1, 3, Tietjen 1984). The disturbed sites include HEBBLE (Thistle & Sherman 1985, Thistle et al. 1985, Thistle et al. 1995), the Madeira Abyssal Plain (MAP, Rice & Lambshead 1994, Thistle et al. 1995) and the Venezuela Basin Stn 2 (VB2, Tietjen 1984).

Table 1. The sites, their physical characteristics, mean and standard deviation of the ES(51) rarefaction statistics for the cores, species count from the site, and the number of cores and nematodes on which the analysis is based. SD: standard deviation

Station	Latitude (°N)	Depth (m)	Sedimentation rate (cms ky^{-1})	Mean ES(51)	SD	Species count	Ind. (cores/ nematodes)	Source
Reference Sites								
Porcupine Abyssal Plain (1989)	49	4850	3.0	28.80	2.14	131	6/1256	Santos et al. (1994)
Porcupine Abyssal Plain (1991)	49	4850	3.0	32.92	1.11	156	6/1428	Santos et al. (1994)
Hatteras Abyssal Plain	32	5411		29.95	1.05	88	2/507	
Venezuela Basin 1	15	3858	2.9	27.21	2.04	54	2/309	Cole et al. (1985)
Venezuela Basin 3	13	3517	4.6	32.13	0.98	85	2/425	Cole et al. (1985)
Disturbed sites								
HEBBLE Stn 1	40	4626		24.94	2.98	133	8/1331	
HEBBLE Stn 2	40	4626		25.26	1.40	124	9/1152	
Madeira Abyssal Plain	31	4950	0.1–1.0	25.39	1.21	78	6/578	Weaver & Rothwell (1987)
Venezuela Basin 2	13	5054	7.2	31.78	2.19	73	2/270	Cole et al. (1985)

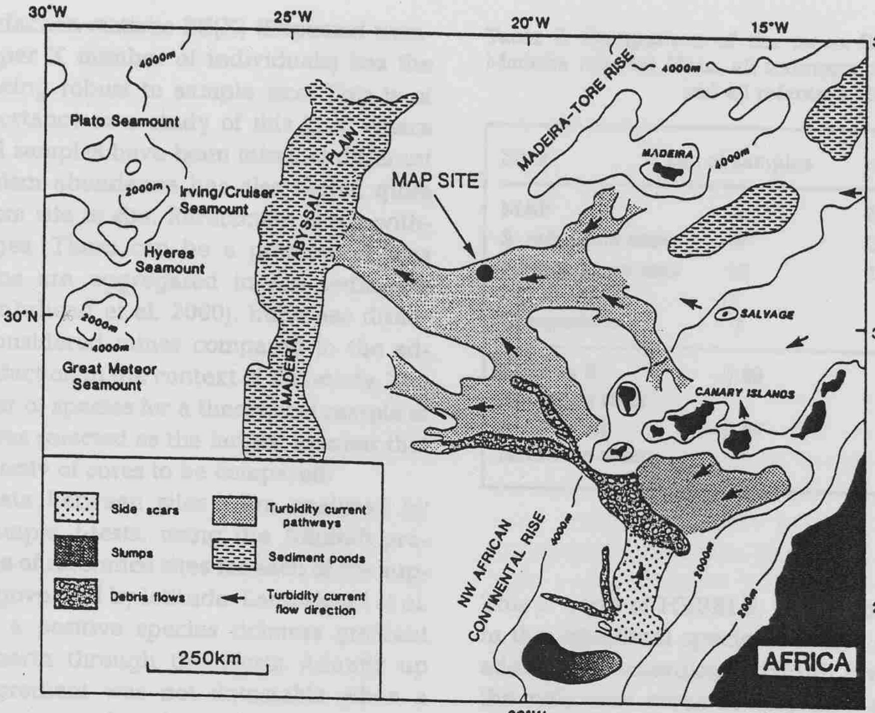

Fig. 1. Map of the Madeira Abyssal Plain (MAP) turbidite region showing the location of the collecting site and the extent of the turbidite (adapted from de Lange et al. 1987)

The PAP site is located to the southwest of Ireland at 48° 50′ N, 16° 30′ W. It receives a seasonal input of aggregated phytodetritus. The HAP site is at 32° 29.6′ N, 70° 21.0′ W. The sediments were hemipelagic, grey-brown terrigenous silt clays with some fine Foraminifera remains.

The 3 sites from the Venezuela Basin represent 3 major sedimentary provinces (Richardson & Young 1987). The pelagic site (VB1) is located at 15° 07′ N 69° 22′ W. Sediments at this site consist primarily of foraminiferan tests, coccolith plates and pteropod shells. The turbidite site (VB2) is located at 13° 45′ N 67° 22′ W. Sediments here consist of alternating layers of pelagic clays and coarse turbidite deposits. The main source of the non-carbonate sediments is discharge from the Orinoco and Amazon Rivers (Bowles & ~~Fleickes~~ 1985■). The deep Venezuela Basin is a low energy environment with restricted renewal at depth (Kinder et al. 1985). The hemipelagic site (VB3) is located at 13° 30′ N 64° 45′ W. Sediments here are a mixture of terrestrially derived clay-size particles mixed with pelagic carbonate sediments. 'HEBBLE' in this paper refers to the stations used for the preliminary studies of the High Energy Benthic Boundary Layer Experiment (Holister & Newell 1991). The stations are in a productive area, which suffers from benthic storms 8 to 10 times yr^{-1} when water velocities 10 m above the sediment reach 15 to 40 cm s^{-1} (Weatherly & Kelly 1982). The MAP station (Fig. 1) lies on the distal part of turbidite deposits (Weaver & Rothwell 1987). This area has been subject to many turbidite events during interglacial-glacial transitions, the last being dated to 930 BP. This most recent turbidite has covered the area of the station with displaced sediment to a depth of at least 90 cm (Thomson & Weaver 1994).

Note that only samples judged adequately quantitative, i.e. from spade-box or deep-sea meiofauna corers, were employed.

Analysis. The nematodes used were identified in just 2 laboratories to ensure comparability given the primitive nature of deep-sea nematode taxonomy. Western Atlantic sample organisms were identified at the City College of New York and eastern Atlantic samples at The Natural History Museum, London. HEBBLE nematodes were originally identified into species at Florida State University, but the Florida collection was later taxonomically calibrated against the collections in the museum.

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The species-abundance data for each core were converted into rarefaction diversity indices using the methods of Sanders (1968) as modified by Hurlbert (1971), employing the BDPro program. Ecological diversity indices are widely used to detect disturbance when working at the alpha-diversity level, although their use is not without controversy, e.g. Gage & May

(1993). The rarefaction statistic ES(X) (Expected number of Species per X number of individuals) has the advantage of being robust to sample size. This is of paramount importance in a study of this kind where differently sized samples have been taken at different sites and organism abundance has also varied quite considerably from site to site. Rarefaction is not without disadvantages. There can be a problem of bias where organisms are aggregated in the sediments (Gray 2000, Lambshead et al. 2000), but these disadvantages are considered minor compared to the advantages of rarefaction in the context of this study. The expected number of species for a theoretical sample of 51 individuals was selected as the largest number that allowed the majority of cores to be compared.

Rarefaction data between sites were analysed by parametric 2 sample *t*-tests, using the *Minitab* program. The choice of reference sites for each of the supposed sites was governed by latitude. Lambshead et al. (2000) reported a positive species richness gradient from south to north through the North Atlantic up to 56° N. This gradient was not detectable when a diversity index was employed as an alpha diversity measure. Nevertheless, the possibility of bias due to latitude was considered when choosing reference stations.

RESULTS

HEBBLE

The mean ES(51) for the 17 cores at the 2 HEBBLE stations had a significantly lower diversity than the reference sites, which bracketed HEBBLE by latitude to the north and south (PAP and HAP), Table 2. However, 12 of the 14 reference cores were taken from PAP. This is north of HEBBLE, so the possibility of bias due to the latitudinal species richness gradient had to be addressed. Accordingly, HEBBLE was compared to all the reference cores adding in 6 additional southern cores, some of which were more than 25° south of HEBBLE. Again, a significantly lower diversity was found at HEBBLE. This second test is conservative, as the majority of the reference cores were found to the south of HEBBLE. The lower diversity, although statistically highly significant, was small with diversity being an ES(51) of approximately 25.1 as opposed to 30.5.

Table 2. Comparison of the mean ES(51) diversity at HEBBLE, the Porcupine Abyssal Plain, the Hatteras Abyssal Plain and all reference sites

Sites	No. of samples	Mean	SD
HEBBLE	17	25.11	2.21
PAP/HAP	14	30.73	2.52
All Reference Sites	18	30.49	2.61
Comparison	**T**	**DF**	**P**
HEBBLE vs PAP/HAP	6.52	26	0.0000
HEBBLE vs all reference sites	−6.60	32	0.0000

Table 3. Comparison of the mean ES(51) diversity at the Madeira Abyssal Plain, all reference sites south of Madeira and all reference sites (S)

Sites	No. of samples	Mean	SD
MAP	6	25.39	1.21
S. reference sites	6	29.76	2.47
All reference sites	18	30.49	2.61
Comparison	***t***	**df**	**p**
MAP vs S. reference sites	−3.89	7	0.0061
MAP vs all reference sites	−6.47	18	0.0000

Madeira Abyssal Plain (MAP)

The mean ES(51) for the 6 cores of MAP site was compared to the 6 reference cores that came from sites located to the south of MAP (Table 3). This is a conservative test, as any latitudinal bias would act to reduce the diversity of the southern cores. MAP cores showed significantly lower diversity than the reference cores but, again, the difference in diversity was modest. For completeness, the mean of the MAP cores was tested against the mean of all the reference cores, with a similar result.

Venezuela Basin Site 2

Only 2 cores were available from this site so statistical analysis would not be appropriate. However, the mean diversity for ES(51) of approximately 31.78 is higher than all the reference cores (30.49) or just the subset of southern reference sites (29.76). It may be concluded that the limited data show no evidence of low diversity at VB2.

DISCUSSION

HEBBLE shows evidence of a low diversity, although the difference between HEBBLE and the reference stations is modest. The one feature that distinguished HEBBLE from the reference cores was the benthic storms reported at this site. Shallow water nematodes are known to be robust to physical disturbance, compared with macrofauna, but not immune as physical disturbance is known to cause modest changes in diversity (Schratzberger & Warwick et al. 1998). The most likely explanation for HEBBLE having a statistically significant, slightly lower diversity than the reference stations are the benthic storms that are associated with this site.

Greater robustness of nematodes to physical disturbance than macrofauna probably explains why no reduction in nematode diversity caused by water currents was reported for Rockall Trough nematodes (Lambshead et al. 1994), despite the evidence of a physical impact on polychaete diversity at this site (Paterson & Lambshead 1995). The Rockall water currents are less energetic than those found at HEBBLE.

The cores from MAP showed a similar nematode diversity to the HEBBLE area, and again the diversity was significantly less than reference sites. The most parsimonius explanation is that this low diversity was associated with the turbidite that impacted this area. The turbidite appears to have left an impression on nematode diversity patterns after almost 1000 yr that is equal to repeated exposure to high-energy benthic storms: this result is intuitively surprising.

Turbidites are large-scale impacts and the Madeira turbidite covered a considerable area (Fig. 1). So it is possible that there has been insufficient time for nematodes to recolonise the impacted area. Data on the dispersal ability of deep-sea nematodes are lacking but, it may be relevant that this taxon lacks a dispersal larval phase. Polychaetes also display a low diversity at MAP (Glover et al. ~~in press~~), although it is not clear how many deep-sea polychaete species lack a larval dispersal phase. Without more information on deep-sea nematode dispersal mechanisms, it is impossible to assess the credibility of this explanation.

Another, more plausible, explanation is that the Madeira turbidite has caused a long-lasting change in sediment characteristics that is significant for nematodes. Such a change might influence diversity. Etter & Grassle (1992) showed that deep-sea macrofaunal diversity was correlated with sediment diversity and Tietjen (1976) discovered a link between deep-sea nematode diversity and sediment characteristics. This second hypothesis is further supported by sedimentation data. MAP has a low sedimentation rate of 0.1 to 1 cm ky^{-1} (Weaver & Rothwell 1987). Only a thin layer of pelagic sedimentation, approximately 1 to 2 mm thick, could be seen in the cores above the turbidite layer (Gooday pers. obs.).

In contrast, the limited data from VB2, which has also been turbidite affected, show no evidence of an impact on diversity. The sedimentation rate at this site is 7.2 cm ky^{-1} and the turbidite is covered by a 14 cm layer of pelagic sediment (Cole et al. 1985) which is at least 2000 years old. There are 2 key differences between VB2 sediments and MAP station sediments. The first is that the VB tubidite was twice as old, allowing greater time for recolonisation. The second is that the nematodes at VB2 were inhabiting pelagic sediments that had been deposited since the last turbidite, whereas the nematode fauna at MAP were, apart from a superficial layer, in turbidite sediments. Either or both of these factors might explain why nematode diversity at VB2, but not at MAP, seemed to have recovered from the turbidite event but the sediment-change explanation seems more plausible at present.

TABL
4

The data are sufficiently strong to propose the hypothesis that deep-sea nematodes show a modest but statistically significant change in diversity when exposed to large-scale physical disturbance. These data suggest that nematodes appear more robust to such disturbance than macrofauna, especially polychaetes. Evidence from shallow water studies is consistent with this interpretation. The most plausible explanation for the lower diversity at the MAP turbidite site is the long-term change in sediment characteristics at this site but, with the current state of knowledge, low-dispersal ability cannot be ruled out as a mechanism.

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Table 4. ES(51) of the 2 samples from the Venezuela Basin Site 2

Sites	No. of samples	Mean	SD
VB2	2	31.78	2.19

Bull. nat. Hist. Mus. Lond. (Zool.) **66**(2):167–170

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A new species of *Sigambra* (Polychaeta, Pilargidae) from the abyssal plains of the NE Atlantic

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INTRODUCTION

During an intensive study of the benthic communities of the NE Atlantic abyssal plains (Rice *et al.* 1994), a new species of *Sigambra* was identified. It was conspicuous in being one of the more abundant species and certainly the dominant predator. The species was widespread, being recorded from study sites from the Cap Verde Abyssal Plain in the south to the Porcupine Abyssal Plain in the north.

MATERIAL AND METHODS

All specimens were collected using a modified United States Naval Electronics Laboratory. spade box corer (SBC). Samples from the Porcupine, Madeira and Cape Verde Abyssal Plains were sectioned horizontally into 0–1 cm, 1–3 cm and 3–5 cm layers and processed through a number of sieves – 1, 0.5 and 0.3 mm. Samples from the Tagus Abyssal Plain were taken with a vegematically modified box corer and only the inner nine subcores were processed through a 0.3 mm sieve.

MATERIAL STUDIED

Specimens have been deposited in a number of taxonomic institutions and corresponding registration numbers are given below. Abbreviations: AM – The Australian Museum, Sydney; LA – Los Angeles County Museum of Natural History; MNHN – Museum National d'Histoire Naturelle, Paris; BMNH – The Natural History Museum, London; NMNH – National Museum of Natural History, Smithsonian Institution; NMS – The National Museums of Scotland; NMW – The National Museum of Wales; ZH Zoologisches Institut und. Museum, Hamburg; ZMUC – Zoological Museum, Copenhagen.

Holotype: Porcupine Abyssal Plain *Challenger II* Criuse 111: 53201#29 48°51.5' N 16°29.6' W, 4844 m, sediment layer 1–3 cm 0.5mm sieve, 14/4/1994 (BMNH 2000. 1852).

Paratypes: Porcupine Abyssal Plain the following samples centred on 48°50' N 16°30' W in 4850 m:

Discovery Cruise 185: 11908#18: 1–3cm 0.3 mm sieve 1 ind. 28/8/1989.

Challenger II Cruise 79: 52701#5: 1–3 cm, 0.3mm sieve 4 ind.; 1–3cm 0.5mm sieve 2 ind (NMSz: 2000.214).16/5/1991.
52701#9: 1–3 cm 0.5mm 1 ind (ZMH). 17/5/1991.
52701#25: 1–3 cm 0.3mm sieve 1 ind.(MNHN-POLY 53); 0–1 cm 0.5 mm sieve 1 ind (NMW.Z: 2000.070).; 3–5 cm 0.5mm sieve 2 ind (NMNH 186794). 20/5/1991;
52701#29: 1–3 cm 0.3 mm sieve 1 ind. (AM); 1 ind. (ZMUC-POL-1013 21/5/1991.
52701#47 1–3 cm 0.3 mm sieve 1 ind. (LA) 21/5/1991.
Challenger Cruise 111: 53201#23 1–3 cm 0.3 mm 1 ind. 13/4/1994; 53201#26 1–3 cm 0.3 mm sieve 1 ind., 1–3 cm 0.5 mm sieve 2 ind., 3–5 cm 0.3 mm 1 ind. 14/4/1994;
53201 # 29 1–3 cm 0.25 mm sieve 1 ind., 1–3 cm 0.5 mm sieve 1 ind., 3–5 cm 1 mm sieve ind. 14/4/1994;
53205#2 0.3 mm 0–1 cm sieve 1 ind., 3–5 cm 0.5 mm sieve 1 ind., 18/4/94.

Tagus Abyssal Plain centred on 38°N 11°W 5035 m: *Discovery* Cruise 186: SBC365 3 ind. 26/9/1989; SBC366 1 ind. 26/9/1989; SBC367 5 ind. 26/9/1989; SBC368 5 ind., SBC369 2 ind. 27/9/1989; SBC371 2 ind. 28/9/1989.

Madeira Abyssal Plain centred on 31°10' N 21°10' W 4985m: *Discovery* Cruise 194: 12174#35: 1–3 cm 0.3 mm sieve 2 ind.: 1–3 cm 0.5 mm sieve 1 ind.; 3–5 cm 0.5 mm sieve 3 ind. 21/8/1990.
12174#43: 1–3 cm 0.3 mm 1 ind. 22/8/1990.
12174#53: 1–3 cm 0.3 mm sieve 2 ind. 23/8/1990
12174 #60: 1–3 cm 0.3 mm sieve 1 ind. 24/8/1990.
12174#80 0–1 cm 0.3 mm sieve 1 ind.; 5–10 cm 0.5 mm sieve 1 ind. 28/8/90.

Cape Verde Abyssal Plain centred on 20°N 30°W 4500–4600 m: *Discovery* Cruise 204: 12600#32 0–1 cm 0.3 mm sieve 1 ind. 6/10/1994.

In addition the following material was examined: *Sigambra bidentata* Britaev & Saphronova, 1981 Natural History Museum Polychaete Collection Z1986:178–183 (5 paratypes), *Vityaz* Stn 7488 38° 41'N:133° 45'E 1550 m Sea of Japan. *Sigambra gracilis* Britaev & Saphronova, 1981 ZR1986.184–185 (2 paratypes), Vostok Bay, Sea of Japan. *Sigambra phuketensis* Licher and Westheide, 1997 Z1993. 15–16 (2 Paratypes), Bang Tao, W. Phuket Island, Thailand.

TAXONOMIC ACCOUNT

Family **PILARGIDAE**
Genus ***SIGAMBRA*** O.F.Müller, 1858

Species *S. magnuncus* sp. nov.

(Figs 1–5)

DESCRIPTION

Holotype: Length 3.7 mm for 33 chaetigers, greatest width of body 0.3 mm.

Paratypes: Range from length 0.5 mm for 13 chaetigers to 10.5 mm for 50 chaetigers, number of segments depends on size of individual. (Fig. 5).

Body unpigmented; slightly flattened anteriorly, but becoming more rounded posteriorly; anterior chaetigers widest.

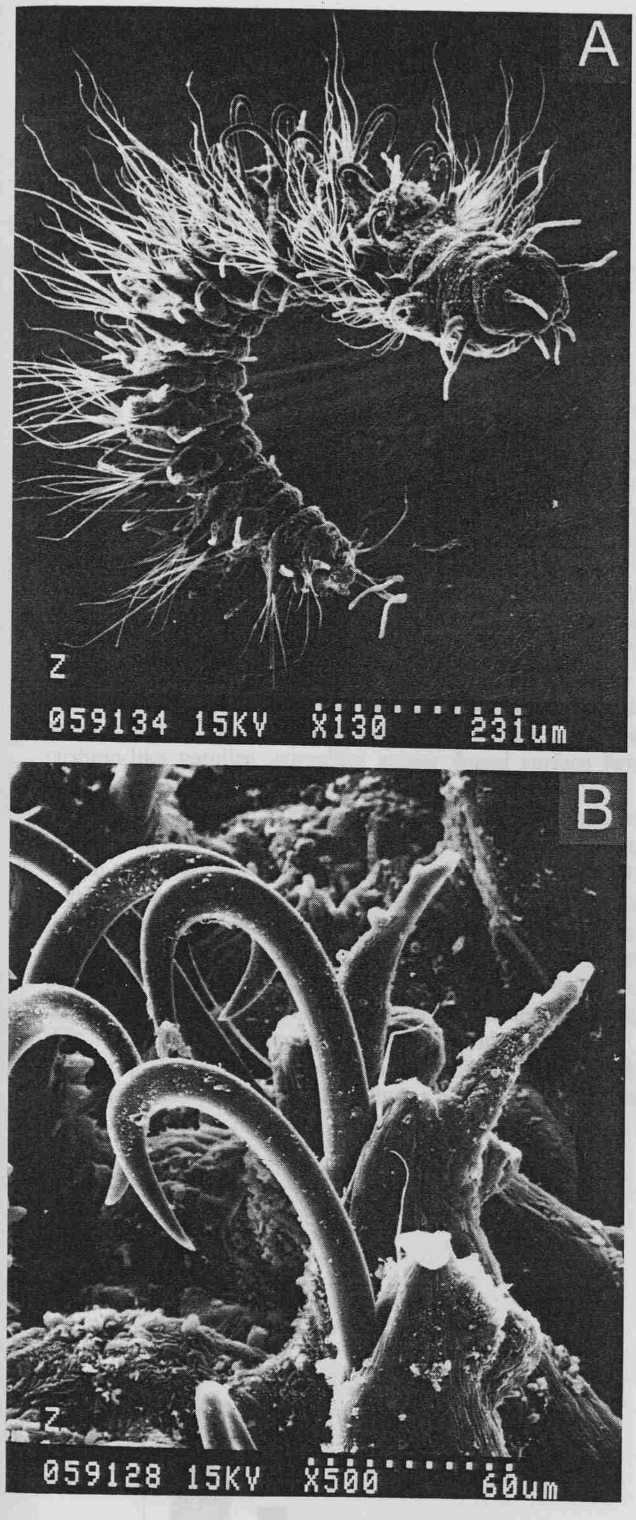

Fig. 1 SEMs of *Sigambra magnuncus* (MAP *Discovery Investigations* 12174#60 0.5 mm sieve, 1–3 cm) A. General view of individual. B. View of notopodia, note the small capillary chaeta in each notopodium

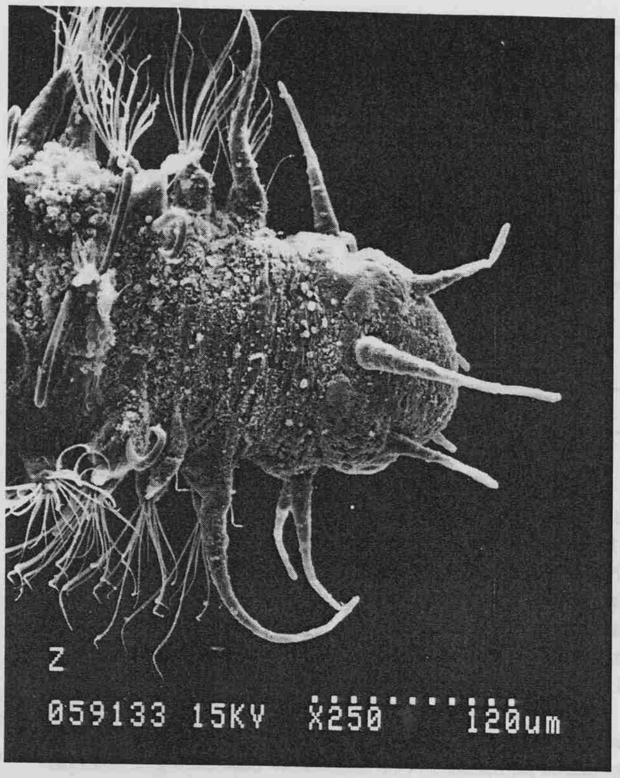

Fig. 2 SEMs of *Sigambra magnuncus* (MAP *Discovery Investigations* 12174#80 0.5mm sieve, 1–3 cm) Dorsal view of anterior region.

Prostomium rounded, slightly indented laterally at insertion of palps and prostomium. Palps biarticulate with relatively long palpostyles; palpophores fused distally over half their length. Three antennae, median antenna longest, situated slightly posterior to laterals in smaller specimens, but more level with them in larger individuals. A pair of cushion like nuchal organs, situated on either side of the median antennae. Eyes absent. Pharynx without jaws, armed with eight equal size, slightly pointed papillae.

Peristomium approximately twice as long as first chaetiger. Two pairs of long tapering tentacular cirri, dorsal cirri longer than ventral, and slightly shorter than median antennae. A row of low cushion-like papillae (sense organs) extending across dorsal surface of peristomium (may only be visible under high magnification).

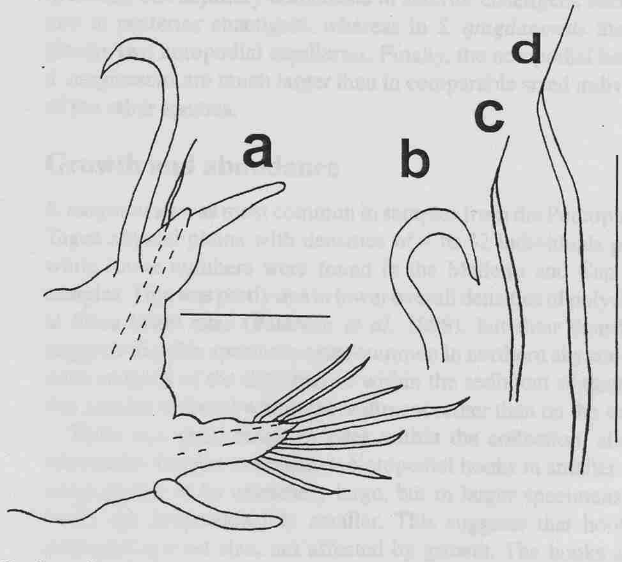

Fig. 3 **a** Parapodium from mid region, anterior view. **b** notopodial hook, **c** & **d** neurocapillaries. Scale bars = 0.1 mm.

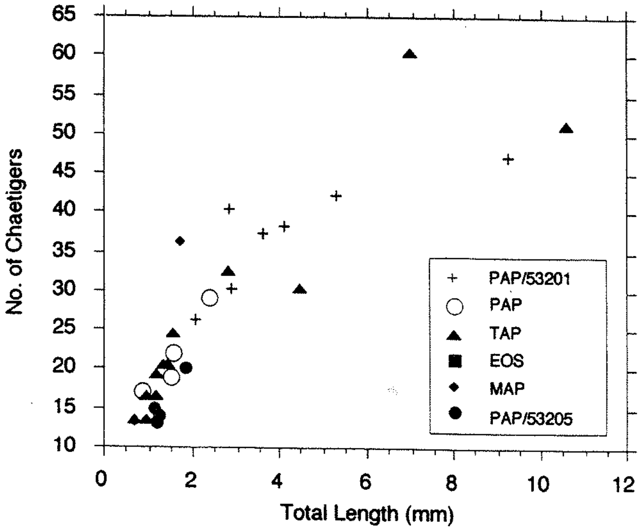

Fig. 4 Graph showing the relationship between size and number of chaetigers. Individuals from different sample sites are identified. PAP–Porcupine Abyssal Plain, MAP – Madeira Abyssal Plain, TAP – Tagus Abyssal Plain, EOS – Cap Verde Abyssal Plain.

Parapodia biramous; anterior parapodia laterally orientated, becoming more dorsal in median and posterior chaetigers. A row of cushion-like papillae extending across dorsal surface between notopodia on each chaetiger.

Notopodia pointed, with straight, blunt-tipped internal aciculae. Dorsal cirri of chaetiger 1 long, thin and tapering; nearly equal in length to median antenna; subsequent dorsal cirri initially shorter with wider bases, but in posterior chaetigers becoming more slender longer and projecting dorsally. Large hooks emergent on chaetiger 3 (Fig. 1b, 2, 3b) until one or two chaetigers from pygidium; in posterior chaetigers hooks meeting in midline. Short, delicate capillaries projecting from most notopodia, just one in anterior chaetigers (Fig. 1b, 3a), usually becoming two in posterior segments.

Neuropodial lobes pointed, with blunt-tipped, straight aciculae (Fig 3a); initially orientated laterally but become more vertical and dorsal in posterior chaetigers. Ventral cirri absent on chaetiger 2; on other chaetigers thin and tapering, equal to or shorter than neuropodia, equal to or slightly longer than dorsal cirri. Neurochaetae simple capillaries, slightly expanded at the base just free of the podia, tips quickly taper into a prolonged point (Fig. 3 c,d).

Pygidium with two tapering cirri. Anus dorsal.

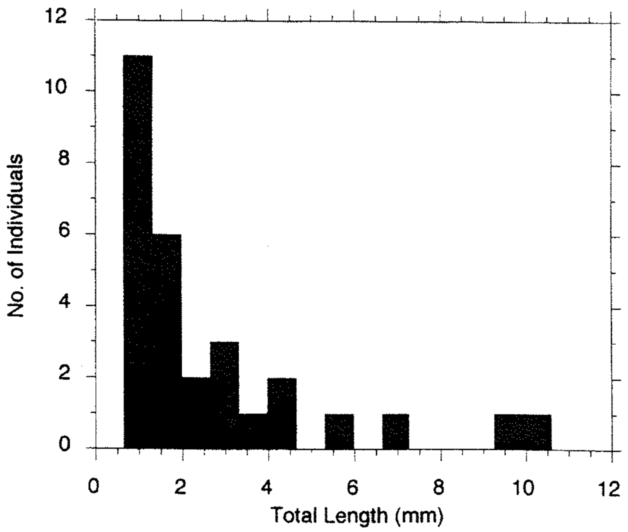

Fig. 5 Histogram showing the range of sizes of *S.magnuncus* collected in the NE Atlantic.

DISTRIBUTION. *S. magnuncus* has been recorded from the abyssal plains of the NE Atlantic at depths from 4000 m to 5085 m.

ETYMOLOGY. The name of this species derives from the large conspicuous hooks on the notopodia (Latin *magnus* – large *uncus* – hook).

DISCUSSION

Taxonomic Affinities

Licher & Westheide (1994) suggested that the Pilargidae was not a separate family and that species in the family belonged in the Hesionidae. This hypothesis has been rejected by Pleijel (1998) and Pleijel and Dahlgren (1998) on the basis that Licher & Westheide's (1994) original study was not rooted in an appropriate outgroup. Subsequent analysis by Pleijel and Dahlgren (1998) indicated that the Pilargidae and Hesionidae were different and non-overlapping groups. We, therefore, retain the family Pilargidae.

Including *S. magnuncus*, there are 17 described species of *Sigambra* (Licher and Westheide, 1997). Based on examination of *Sigambra* material in the NHM and the revision of Licher & Westheide (1997), *S. magnuncus* shares certain features with *S. ocellata* (Hartmann-Schröder, 1959), *S. bidentata* Britaev & Saphronova, 1981 and *S. qingdaoensis* Licher & Westheide, 1997, namely the ventral cirrus is missing on chaetiger 2 and there are eight papillae in the pharynx (Licher & Westheide, 1997). The relative proportions of the dorsal and ventral cirri suggest similarities with *S. ocellata*, however, in *S. magnuncus* the notopodial hooks start on chaetiger 3 rather than chaetiger 6 as in *S. ocellata.* In *S. bidentata* and *S. qingdaoensis* the notopodial hooks can start from chaetigers 3, similar to *S. magnuncus*, but in addition to differences in cirral length, *S. magnuncus* differs from *S. bidentata* in not having bidentate neurochaetae. *S. magnuncus* differs from *S. qingdaoensis* in having one capillary notochaeta in anterior chaetigers, becoming two in posterior chaetigers, whereas in *S. qingdaoensis* there are always two notopodial capillaries. Finally, the notopodial hooks in *S. magnuncus* are much larger than in comparable sized individuals of the other species.

Growth and abundance

S. magnuncus was most common in samples from the Porcupine and Tagus abyssal plains with densities of 4 to 32 individuals per m^2, while lower numbers were found in the Madeira and Cap Verde samples. This was partly due to lower overall densities of polychaetes at these latter sites (Paterson *et al.* 1998), but their distribution suggests that this species is more common in northern abyssal areas. Also analysis of the distribution within the sediment suggests that this species is found within the sediment rather than on the surface.

There is a good range of sizes within the collection, allowing allometric changes to be noted. Notopodial hooks in smaller specimens appear to be extremely large, but in larger specimens these hooks are proportionately smaller. This suggests that hooks are produced at a set size, not affected by growth. The hooks always occur first on chaetiger 3.

Size of specimens ranges from 0.5 to 10.5 mm, although most individuals were between 0.75 to 4.5 mm long (Fig. 5). The relationship between length of specimen and number of chaetigers is given in Fig. 4. The graph indicates that initially as individuals increase in length so the numbers of chaetigers increases linearly, however, at the upper size there is wide variation in numbers of chaetigers, suggesting that there may be an upper limit to chaetiger number.

Growth in *Sigambra grubii* Muller, 1858 also appears to show a linear relationship between length and number of chaetigers over a similar size range as *S. magnuncus* (Salazar-Vallejo, 1990). However, there was more variation in the relationship between size and the chaetiger on which the first hook appeared.

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