INTRODUCTION

Studies in a variety of habitats, both terrestrial and marine, demonstrate a unimodal relationship between productivity and species diversity (e.g., Rosenzweig & Abramsky 1993, Waide et al. 1999). The unimodal curve may occur on regional scales for a broad range of terrestrial taxa, and it is postulated to apply on local to regional scales for deep-sea macrobenthos along bathymetric (and presumed productivity) gradients (e.g., Rex 1981, Rosenzweig & Abramsky 1993, Rosenzweig 1995). While particulate organic carbon (POC)
flux (and hence food availability and community productivity) decreases with increasing water depth in the ocean (e.g. Suess 1980, Martin et al. 1987), many parameters besides productivity often covary with depth, including terrigenous input, current energy, and hydrostatic pressure (e.g. Carney et al. 1983, Gage & Tyler 1991). Thus, diversity changes along an oceanic depth gradient are difficult to ascribe solely to variations in community productivity.

The influence of productivity on the diversity of deep-sea benthos is of particular interest because (1) deep-sea habitats appear to have extraordinary levels of local, and possibly, global diversity (Hessler & Jumars 1974, Grassle & Maciolek 1992, Snelgrove & Smith in press), and (2) the factors controlling these high diversity levels are poorly understood. Any unified theory of species diversity must explain patterns in deep-sea sediments, one of Earth’s largest and potentially most species-rich biotopes (Grassle & Maciolek 1992, Snelgrove & Smith in press).

The abyssal North Pacific provides a useful setting to explore productivity-diversity relationships for at least 2 reasons. POC flux to the seafloor (which controls productivity in most deep-sea habitats) varies dramatically due to equatorial upwelling, while other variables (in particular, depth, continental influences, and hydrodynamic regime) remain relatively constant. In addition, the Pacific abyssal seafloor is the most extensive of deep-sea sedimentary habitats. In this study, we use data from the Joint Global Ocean Flux (JGOFS) Equatorial Pacific Study, and baseline data from nodule-mining impact studies, to investigate (1) the relationship between productivity and local species diversity, and (2) species turnover between sites separated by 200 to 3000 km in the abyssal Pacific.

The causes behind unimodal productivity-diversity relationships are controversial (Rosenzweig & Abramsky 1993, Waide et al. 1999, Levin et al. 2001). Diversity is thought to initially increase with increasing productivity because of a rise in the number of species that can maintain a minimum viable population size. At high levels of productivity, diversity may decrease, possibly due to reduced spatial heterogeneity of food resources, changes in competitive structure, or enhanced environmental stress (Rosenzweig & Abramsky 1993, Levin et al. 2001). Our abyssal study sites range from the extremely food-poor central Pacific gyre (Hessler & Jumars 1974) to the relatively productive equatorial zone (Berelson et al. 1994, Smith et al. 1997); if productivity fundamentally influences species diversity in the deep sea, we predict a strong diversity-productivity relationship across our study sites.

Spatial patterns of species turnover in the abyssal deep sea are very poorly studied. Paterson et al. (1998) found evidence of measurable macrobenthic species turnover over distances of 400 to 3000 km in the abyssal Atlantic and Pacific, although Glover et al. (2001) suggested that spatial differences among the Atlantic sites may be explained by undersampling of the sparse, species-rich abyssal fauna. If species turnover is significant over scales of >1000 km in the abyss as postulated by Paterson et al. (1998), we predict that turnover will be evident even among macrofaunal community dominants on spatial scales of 3000 km in the Pacific abyss.

To test these predictions, we focus on the polychaete component of the macrobenthos because this taxon constitutes the bulk of macrofaunal abundance and species richness at abyssal depths (Paterson et al. 1998, Glover et al. 2001) and because the polychaetes are relatively tractable to detailed taxonomic analyses.

### DESCRIPTION OF STUDY SITES

The EqPac study formed part of US Joint Global Ocean Flux Study, the major goals of which are 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 (Murray et al. 1997). The EqPac samples were collected in November 1992 aboard the RV ‘Thomas Thompson’ at 0°, 2°, 5° and 9° N, 140° W in 4300 to 4900 m of water (Fig. 1, Table 1) (Smith 1992). As part of C. Smith’s EqPac project, a series of box cores were also collected from the Hawaii Ocean Time Series (HOT) station at 23° N, 158° W (Karl & Lukas 1996). The collections were made in August 1992 and February 1993 aboard the RV ‘Moana Wave’.

The manganese nodule-mining province between the Clarion and Clipperton Fracture Zones (CCFZ) was intensively studied as part of the Deep Ocean Mining Environmental Study (DOMES) (Piper & Blueford 1982), the ECHO 1 expedition (Wilson & Hessler 1987) and the Preservational Reserve Area (PRA) study (Wilson 1990, Wilson 1992). We analyzed data 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 DOMES Site A samples were collected aboard the RV ‘Oceanographer’ in 1977/78 as part of a study of the effects of trial mining for manganese nodules. The ECHO 1 samples were collected in 1982 at another test mining area by the RV ‘Melville’ (Spiess et al. 1987). No differences in community structure or diversity were found between test sites and undisturbed control sites, although this may be a consequence of undersampling of the communities (Wilson & Hessler 1987). The PRA samples were collected in 1989 by the RV ‘Moana Wave’ in a baseline study of a site designated as a reserve from any future manganese nodule mining (Wilson 1990, 1992).
Upwelling of nutrient rich water in the central and eastern equatorial Pacific Ocean fuels new biological production that could account for as much as 25 to 50% of the total global value (Chavez & Barber 1987). Images from the SeaWiFS ocean color sensing satellite demonstrate that the band of equatorial productivity extends from the coast of Ecuador to at least 150°W. The EqPac sites at 0° N, 2° N and 5° N lie within the influence of equatorial upwelling, while the remaining sites lie in the central north Pacific oligotrophic gyre region (Smith et al. 1997, Smith & Demopoulos in press). Estimates of averaged annual primary productivity, taken from the Rutgers University Ocean Primary Productivity group website (http://marine.rutgers.edu/opp/), and based on SeaWIFS data, are provided in Table 1 (Behrenfeld & Falkowski 1997). Data on deep POC flux, as reported in Smith et al. (1997), are also provided in Table 1. No POC flux measurements were available for the CCFZ sites, although their surface productivity regimes and sediment characteristics are similar to those at the EqPac 9° N site, which also lies within the CCFZ manganese nodule zone.

The presence of substantial amounts of fresh phytoplankton detritus (or phytodetritus) has been recorded at the EqPac 0° N, 2° N and 5° N sites, but not at any of the other EqPac sites, or in the CCFZ region (Smith et al. 1996). The authors concluded that this phytodetritus was an important food source for benthic microbes and metazoans. Rates of bioturbation are higher at 0 to 5° N than at 9° N and macrofaunal abundance along the EqPac transect is strongly correlated with deep POC flux (Smith et al. 1997).

**MATERIALS AND METHODS**

**Sample collection and processing.** All the samples were collected using a USNEL spade box core (Hessler & Jumars 1974). Samples were washed on a 300 µm sieve, fixed in 10% formalin for >24 h and transferred to 70 to 80% ethanol for permanent storage. Standard box core washing methods developed by R. Hessler (Hessler & Jumars 1974) were used on all cruises. In the laboratory, all the macrofaunal specimens were taken out and polychaetes were first sorted to family, and then to the species level. The specimens from DOMES A were identified by K. Fauchald, those from ECHO 1 and PRA by K. Fitzhugh and those from EqPac and HOT stations by A. Glover. Species identifications for the DOMES A specimens were cross-checked with the remaining CCFZ specimens by K. Fitzhugh. The EqPac and HOT specimens have not been cross-

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**Table 1.** Site, position depth, number of USNEL spade box core samples, averaged annual surface productivity (Behrenfeld & Falkowski 1997), deep POC flux estimates (Smith et al. 1997), mean abundance of polychaetes per 0.25 m² and total number of species. Note that only polychaetes identified to species level are included in the abundance calculation. All sites significantly different in terms of abundance per 0.25 m² (ANOVA p < 0.05), except 0° N and 5° N, 2° N and 5° N, 2° N and PRA, 9° N and DOMES A, 23° N and 9° N, 23° N and DOMES A.

<table>
<thead>
<tr>
<th>Site</th>
<th>Position</th>
<th>Depth (m)</th>
<th>No. of box cores</th>
<th>Average annual surface productivity (g C m⁻² yr⁻¹)</th>
<th>POC flux at 2000 m (g C m⁻² yr⁻¹)</th>
<th>Abundance 0.25 m² (SE)</th>
<th>No. of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>EQPAC 0° N</td>
<td>0° N, 140° W</td>
<td>4300</td>
<td>3</td>
<td>230</td>
<td>1.6</td>
<td>84 (27.9)</td>
<td>73</td>
</tr>
<tr>
<td>EQPAC 2° N</td>
<td>2° N, 140° W</td>
<td>4400</td>
<td>4</td>
<td>200</td>
<td>1.3</td>
<td>66 (6.4)</td>
<td>82</td>
</tr>
<tr>
<td>EQPAC 5° N</td>
<td>5° N, 140° W</td>
<td>4400</td>
<td>3</td>
<td>155</td>
<td>1.4</td>
<td>80 (19.1)</td>
<td>76</td>
</tr>
<tr>
<td>EQPAC 9° N</td>
<td>9° N, 140° W</td>
<td>4900</td>
<td>3</td>
<td>140</td>
<td>0.44</td>
<td>13 (2.3)</td>
<td>23</td>
</tr>
<tr>
<td>HOT 23° N</td>
<td>23° N, 158° W</td>
<td>4800</td>
<td>4</td>
<td>105</td>
<td>0.4</td>
<td>9 (1.7)</td>
<td>14</td>
</tr>
<tr>
<td>DOMES A</td>
<td>8° 27' N, 150° 47' W</td>
<td>5100</td>
<td>47</td>
<td>140</td>
<td>N/A</td>
<td>16 (0.8)</td>
<td>104</td>
</tr>
<tr>
<td>PRA</td>
<td>12° 57' N, 128° 19' W</td>
<td>4800</td>
<td>16</td>
<td>130</td>
<td>N/A</td>
<td>65 (16.8)</td>
<td>100</td>
</tr>
<tr>
<td>ECHO 1</td>
<td>14° 40' N, 126° 25' W</td>
<td>4500</td>
<td>15</td>
<td>135</td>
<td>N/A</td>
<td>42 (5.5)</td>
<td>113</td>
</tr>
</tbody>
</table>
checked with the CCFZ specimens, and remain as a separate dataset in this analysis. Unique species code numbers were assigned to distinguish species unknown to science.

Analysis of species diversity. We investigated 2 types of species diversity differentiated by the spatial scale considered: (a) local or within-site, diversity, sometimes referred to as alpha diversity, and (b) species turnover between sites, which some authors have termed beta diversity (Whittaker 1972, Gray 2000). We measured local diversity as the diversity of a single site (e.g. EqPac 0°N), encompassing the total diversity of sampling units (box cores) at that site. We evaluated species turnover by analyzing the similarity of sites in terms of species composition based on species lists, and the distribution of individuals among species, using multivariate and parsimony methods. The spatial scale at which turnover was analyzed was determined by the distance between sites, in this case ranging from 200 to 3000 km.

Species diversity analysis was undertaken using Biodiversity Pro (McAleese et al. 1996). Shannon $H'$ and rarefaction analysis were used as measures that are sensitive to both equitability and richness while being relatively sample size independent (Sanders 1968, Hurlbert 1971, Fager 1972, Gage & May 1993). The term ‘species diversity’ is used throughout this paper to indicate measures of diversity that incorporate both equitability and richness. Regression analysis was carried out using Statview 5.0. PAUP v.3.0 (Swofford 1993) was used to classify sites based on species presence and to graphically illustrate comparative species richness using the parsimony method (Lambshead & Paterson 1986, Glover et al. 2001). The Normalized Expected Species Shared (NESS) measure of faunal similarity was calculated using the computer program COMPAH96 (http://www.es.umb.edu/edgwebp.htm). This computer program uses a modified version of the original NESS calculation (NNESS) (Grasse & Smith 1976).

RESULTS

Local diversity

From the EqPac and HOT sites, a total of 177 polychaete species were recorded from 2.94 m² of seabed; from the DOMES A, ECHO 1 and PRA sites in the CCFZ region, the total was 183 species from 21 m² of seabed (Table 1). 70% of identifiable specimens could be assigned to known genera, but only about 5 to 10% could be identified as a previously named species; thus, the vast bulk (>90%) of the collected polychaete species are undescribed taxonomically (i.e. they are new to science). The polychaete assemblage was highly dominated by the families Cirratulidae (~17%), Spionidae (~17%), Paraonidae (~17%), Sabellidae (~10%) and Syllidae (~10%) at all stations. These were also the most speciose families. The highest polychaete abundance occurred at the EqPac 0° N, 2° N and 5° N sites, and the lowest at the 9° N site, the HOT site and the DOMES A site. Polychaete abundance at the PRA site was similar to that at the EqPac 2° N, and that at the ECHO 1 site fell midway between the high-POC flux EqPac sites (0° to 5° N) and the oligotrophic DOMES A site. The greatest number of species was found at the most intensively sampled site, DOMES A, while the lowest number of species were found at the HOT station, where both abundance and sampling intensity were low (Table 1).

To account for variability in both species abundance and sampling intensity, the Shannon diversity index ($H'$) and rarefaction methods were used. $H'$ may be sensitive to sample size, i.e. to the number of individuals in a sample (Lambshead et al. 1983, Soetaert & Heip 1990). The relationship between $H'$ and the abundance of polychaetes per box core in our data (Fig. 2) indicates that, below a level of approximately 35 individuals per box core, $H'$ is strongly density-dependent. Above this level, $H'$ ranges from 0.96 to 1.6, but little variability is explained by abundance, indicating that $H'$ has become relatively density-independent.

Given the apparent density-independence of $H'$ in the higher-abundance samples, the diversity statistic was calculated for only those samples containing
greater than 35 individuals (Fig. 3). This excluded samples from very oligotrophic regions at 9° N, HOT and DOMES A. The EqPac 0° N, 2° N and 5° N sites showed the highest diversity when measured in this way; species diversity at the CCFZ sites ECHO 1 and PRA was significantly lower, and it was significantly lower at PRA than at ECHO 1 (Fig. 3).

In a similar analysis using rarefaction at a sample size of 30 individuals \([E(S_{30})]\) on replicate box cores, the EqPac 0° N, 2° N and 5° N sites again show higher diversity than the CCFZ sites (Fig. 4).

The rarefaction analysis was also conducted on pooled samples (Fig. 5). EqPac 2° N shows the highest diversity (82 species for 163 individuals) followed by 5° N (75 species for 163 individuals), 0° N (71 species for 163 individuals), ECHO 1 (60 species for 163 individuals), DOMES A (56 species for 163 individuals) and PRA (47 species for 163 individuals).

In order to evaluate directly the relationship between POC flux, or appropriate proxies, and polychaete species diversity, a relatively low E(S) value was selected so that the 9° N and HOT 23° N sites could be included. No deep POC flux data are available for the CCFZ sites so we used macrofaunal abundance (no. m\(^{-2}\)) as a proxy for POC flux. A number of studies have documented a strong positive correlation between POC flux and macrofaunal abundance in the deep sea (Sibuet et al. 1989, Cosson et al. 1997, Smith et al. 1997, Etter & Mullineaux 2001, Glover et al. 2001, Smith & Demopoulos in press); polychaetes typically make up 60 to 70% of deep-sea macrofaunal abundance (e.g. Smith & Demopoulos in press), justifying their use as a flux proxy. At E(S\(_{20}\)), there was no obvious relationship between either POC flux or polychaete abundance and polychaete species diversity across our sites (Fig. 6).

**Species turnover**

Using the principle of maximum parsimony (Lambasthead & Paterson 1986, Bellansantini et al. 1994, Glover et al. 2001), the abyssal sites were classified according to species presence (Fig. 7). In the EqPac region, the 3 sites lying under the influence of equatorial upwelling (also the spatially closest sites) form a unique group, strongly supported by 21 species which occur at all 3 sites. In the CCFZ region, the 2 spatially closest sites, ECHO 1 and PRA, formed a unique cluster, supported by 25 species. All sites exhibit a long tail of rare species that were collected at only a single site. These species are hereafter termed ‘unique’ species.

Multivariate analysis using NNESS (which takes into account the relative abundance of both rare and abundant species) further supports this geographic grouping (Fig. 8). For the EqPac sites, percentage similarity varies from 30 to 70% at \(m = 5\) (where \(m\) is the subsample size used to calculate NNESS) and from 25 to 65% at \(m = 15\). Higher values of \(m\) are more sensitive
to the contribution of rare species; as $m$ approaches 1, the analysis converges to the Morista-Horn presence/absence index (Gallagher 1996). As would be expected, increasing the sensitivity to rare species reduces the overall similarity; at $m = 15$, EqPac 9° N and HOT 23° N sites no longer form a supported group, probably because the total species pool is poorly sampled at these sites due to small sample sizes and faunal densities.

In the CCFZ region, the 2 physically closest sites, ECHO 1 and PRA, form a consistent cluster, at both high and low values of $m$. When only dominant species are taken into account ($m = 10$), all sites show similarity levels of 73 to 74%, including DOMES A and PRA, which are separated by 2700 km. When the influence of rare species is included at $m = 200$, the similarity level of DOMES A and PRA drops to 56%.

At each site, a certain proportion of individuals fall into species that may be termed ‘unique’, ‘widespread’ or ‘ubiquitous’. Unique species are those that were collected at 1 site only, widespread species are defined as occurring in at least 2 sites, and ubiquitous species were recorded at all sites within a data set (i.e. EqPac or CCFZ stations). In terms of species composition (Fig. 9a), each site contained a substantial proportion of unique species, varying from 20% at PRA to over 50% at 2° N. However, in general, the majority of species found at any single site were widespread or ubiquitous across sites separated by 200 to 3000 km.

When abundance is taken into account (Fig. 9b), this pattern is reinforced, with 70 to 90% of individuals belonging to widespread or ubiquitous species. In other words, at all sites within each data set, the fauna is dominated by a core group of the same, abundant species. The many rare species make only a small contribution (~10 to 30%) to the overall abundance of polychaetes at any site.

**DISCUSSION**

**Relationship between productivity and diversity at local scales**

The highest local diversity was recorded at EqPac sites 0°N, 2°N and 5°N (Figs. 3, 4 & 5). These sites showed significantly higher diversity than the sites in the CCFZ region. However, when POC flux is plotted against local diversity at $E(S_{20})$, no clear relationship between diversity and productivity is evident (Fig. 6a). Furthermore, including the data from the CCFZ, and plotting polychaete abundance (a proxy for deep POC flux) against local diversity also shows no obvious pattern.

Small sample sizes at 9° N and HOT 23° N may be obscuring a productivity-diversity relationship. At low $E(S_n)$ levels, rarefaction is more sensitive to evenness than to species richness. Sites can show similar levels of evenness, but in fact display differing overall species richness (Gage & May 1993). When higher levels of $E(S_n)$ are used (Fig. 5a), and the 9° N and HOT sites excluded, diversity is significantly higher at the more productive sites.

Slightly higher species diversity at the 0 to 5° N sites compared to those in the CCFZ region, does not however, imply a strong ‘relationship’ between productiv-
ity and diversity, as has been reported in other ecosystems. For terrestrial plants, monotonic decreases in diversity with increasing productivity have been reported in small-scale plots (Huston 1979, Tilman 1982). At larger scales, a unimodal pattern has been reported for small mammals (Rosenzweig & Abramsky 1993) and freshwater zooplankton (Rosenzweig 1992).

Ocean depth has traditionally been viewed as a useful inverse proxy of benthic productivity. For this reason, studies of depth-related diversity patterns have been used to explore relationships between productivity and diversity (Rex 1973, 1977, 1981, Huston 1979, Lambshhead 1993, Rosenzweig 1995, Cosson-Sarradin et al. 1998). In the cited studies, diversity appears to peak at depths between 2000 and 3000 m. While this pattern is consistent with a unimodal productivity versus diversity relationship, many other depth-varying factors could lead to a bathyal peak in diversity. These include bathymetric boundary constraints (Pineda & Caswell 1998), variations in sediment grain-size diversity (Etter & Grasse 1992), large-scale habitat mosaics resulting from submarine canyons and turbidity flows (Levin et al. 2001), variable current regimes, historical contingencies (Etter et al. 1999, Rogers 2000) and latitudinal effects (Rex et al. 1993, 1997, 2000). It is far from obvious that productivity plays an important role in this process.

The central equatorial Pacific abyssal plain is a much simpler system in which to test productivity-diversity relationships in the deep sea, because many variables (e.g. depth, terrigenous input, hydrodynamic regime) appear to be relatively constant. We find weak support for a monotonic increase in diversity with productivity, and no evidence of a unimodal relationship, as predicted from a number of ecological studies (Fig. 6) (Huston 1979, Rosenzweig 1995). We can extend the deep-sea productivity versus diversity analysis across basins by including data from the North Atlantic abyss, and using a rarefaction sample size more sensitive to species richness ($E(S_{80})$) (Fig. 10). We still find that only
about 20% of the variance in diversity may be explained by productivity, when using polychaete abundance as a proxy for POC flux. It should be noted that our abyssal Pacific stations span a 4-fold dynamic range in productivity; this is comparable to the productivity range over which unimodal diversity patterns have been documented for terrestrial systems (Rosenzweig & Abramsky 1993, Rosenzweig 1995). In addition, the lower end of our productivity range falls in the oligotrophic abyss, one of the least productive habitats on the Earth’s surface (Hessler & Jumars 1974, Smith & Demopoulos in press). If very low productivity universally depresses local species diversity, the effect is modest in the oligotrophic abyssal Pacific.

We suspect that variations in diversity in the abyssal Pacific, and the abyss worldwide, are created by a suite of local and regional factors. For example, on the EqPac JGOFS benthic leg in 1992, the 0 to 5°N sites were characterized by the presence of recently-accumulated phytodetritus deposits (Smith et al. 1996), increased bioturbation activity (Smith et al. 1997), increased microbial biomass (Smith et al. 1997) and altered sedimentary characteristics in the form of larger grain size and a higher proportion of foraminiferal tests relative to 9°N (Berelson et al. 1994, Stephens et al. 1997). Measurable quantities of chlorophyll a, excess 234Thorium, phytoplankton with intact chloroplasts and high respiration rates at EqPac 0°N, 2°N and 5°N (Smith et al. 1997) contrast sharply with the relatively refractory nature of sediments at 9°N, and our sites in the CCFZ region.

Other studies document a small but apparently significant decrease in nematode diversity from the high-flux 0°N to 5°N region to the low flux 9°N region (Brown et al. 2001, Lambshead et al. 2002). They attributed higher diversity at 0 to 5°N to the presence of phytodetritus.

Patchy deposition of ephemeral resources (e.g. phytodetritus), has been postulated to promote local species diversity in the deep sea (e.g. Grassle & Morse-Porteous 1987, Grassle 1989, Grassle & Maciolek 1992, Snelgrove & Smith in press). In particular, phytodetrital collection in seafloor depressions and burrows could yield a spatial mosaic that increases diversity on local scales (Grassle & Maciolek 1992). Thus, the occurrence of phytodetritus at the EqPac stations from 0 to 5°N (Smith et al. 1996) might explain the higher local diversity at these stations.

The potential influence of phytodetritus at 0 to 5°N must be treated with caution, however. Phytodetritus has only been recorded at these locations during a single cruise (Smith et al. 1996). The wide distribution of the phytodetritus (across 10 degrees of latitude) indicates that it was created by a large-scale bloom; the frequency of occurrence of phytodetritus in the equa-
torial Pacific, however, remains to be evaluated. Ascribing regional differences in diversity in the abyssal Pacific to the presence or absence of phytodetriritus is premature.

Associated with enhanced productivity at 0 to 5°N 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 10-fold greater at 0 to 5°N compared to 9°N (Smith et al. 1997). Megafaunal abundances, and very likely bioturbation rates, are also much lower at the CCFZ sites than at the 0 to 5°N stations (Tilot 1991, Smith & Demopoulos in press, C. Smith pers. obs.). Evidence from studies in both deep and shallow-water have shown that localized small-scale disturbance may increase diversity (Connell 1978, Sousa 1979, Smith 1986, Kukert & Smith 1992, Widdicombe & Austen 1999, Snelgrove & Smith in press). In the abyssal Pacific, where rates of disturbance are likely to be very low, enhanced megafaunal activities and bioturbation, such as observed at 0 to 5°N, seem particularly likely to shift communities towards intermediate levels of disturbance and enhanced diversity (Huston 1979). In situ studies are required, however, to determine whether urchin burrowing disturbance enhances local species diversity at the 0 to 5°N stations.

It has been suggested that deep-sea datasets may provide some of the best evidence for productivity-diversity relationships (Rosenzweig 1995). In the abyss, isolated from the influences of depth and terrigenous inputs, we find no evidence for a unimodal relationship between productivity and diversity, and only weak evidence that extremely low productivity may reduce diversity (Fig. 10). While variability in abyssal diversity exists, it cannot be explained exclusively by a single environmental factor such as productivity. As for terrestrial habitats (Rohde 1992), we expect that deep-sea diversity is ultimately controlled by a suite of local and regional factors.

**Species turnover in the central Pacific abyss**

Evaluating species turnover in deep-sea samples requires teasing out the effects of under-sampling. We have used 3 approaches: (1) examining the species composition in terms of presence/absence using the principle of maximum parsimony (Fig. 7), (2) investigating the influence of common and rare species on
Differences between sites could result from an essentially similar mobility of the average deep-sea polychaete will be less than that of this abyssopelagic scavenging amphipod, the presence of undetected cryptic species may depress our estimates of diversity.

Along the EqPac transect, nematode species turnover is thought to be high, with a distinct 'phytodetrital' fauna at 0 to 5°N (Brown 1998, Lamb-Head et al. 2002). For nematodes at least, areas such as the central Pacific may be subdivided into distinct biogeographical zones, dependent on the dynamics of the upper ocean ecosystem and the amount and quality of export production (Smith et al. 1997).
appear to be faunistically very similar, differing primarily in the make up of the rare species pool. However, further sampling efforts are needed, using both morphological and molecular approaches, to determine whether ‘rare’ species actually have very widespread distributions and are simply undersampled. If further sampling efforts reveal a unique, endemic fauna at each site, closely related to between-site distance, then species turnover for polychaetes may be as high as that for nematodes, and species extinction might be a significant risk from large-scale anthropogenic disturbances, such as manganese-nodule mining (ISA Sanya report 1998).

Comparative species richness of the equatorial Pacific abyss

Local diversity of polychaetes in the central equatorial Pacific abyss is clearly very high. \( E(S_{30}) \) at a single site in the Pacific abyssal Peru Basin was in the range 18 to 22 (Borowski & Thiel 1998), which is similar to our CCFZ sites, and lower than at the productive EqPac sites (e.g. \( E(S_{30}) = 24.5 \) at 0° N (Fig. 4)). Levin & Gage (1998) report \( E(S_{30}) \) values of 3 to 23 for slope depths of 220 to 3400 m in the Pacific and Indian Oceans; these values fall below those from the EqPac 0 to 5° N sites. Hessler & Jumars (1974) also report lower \( E(S_{30}) \) values of 12 to 18 at the 5600 m depth CLIMAX II locality in the central Pacific gyre.

Grassle & Maciolek (1992) reported a total of 798 species from 21 m² on the northwest Atlantic slope at depths ranging from 1500 m to 2500 m. Of those 798 species, 385 species (45%) were polychaetes. In the present study, 183 species of polychaetes were recorded from 19.25 m² at CCFZ and 177 species from 2.94 m² at EqPac. The number of individuals (sample size) is much lower in the abyssal Pacific sites, so these figures are not directly comparable. Grassle & Maciolek (1992) reported that for 1000 polychaete individuals, there were approximately 90 to 100 species. At the PRa site, where 1043 polychaetes were identified, 100 species were found, a comparable level of diversity. At EqPac 2° N, 83 species were found from just 163 individuals, suggesting substantially higher diversity. Thus, in the Pacific abyss, diversity is comparable to the highest levels of diversity found on the North Atlantic slope, and beneath equatorial upwelling such as at 0 to 2° N, diversity appears to be higher. We await further studies of polychaete taxonomy, species ranges and reproductive biology before extrapolating further to estimates of global polychaete diversity. However, even with low levels of species turnover, the vastness of the central Pacific abyss may cause it to be one of the most speciose benthic regions on the planet.

Conclusions

Our data lead to the following conclusions. (1) The relationship between productivity and diversity in the Pacific abyss is not unimodal, and at most weakly increasing, suggesting that extreme oligotrophy does not limit local diversity in the deep sea. (2) For macrofaunal community dominants, there is very low turnover at scales of up to 3000 km in the abyssal equatorial Pacific. However, for rare species, turnover could be very high, but our sampling intensity is inadequate to draw firm conclusions. More intensive sampling, as well as improved taxonomic resolution, is required to resolve this issue. (3) Local species richness in the central equatorial Pacific abyss is higher than that recorded at abyssal depths in the north Atlantic, and comparable to levels from north Atlantic slope depths. For sites lying under the productive EqPac 0 to 5° N sites, polychaete diversity, measured by rarefaction, is the highest yet recorded for the deep sea, suggesting high species diversity in the Pacific compared to the Atlantic.

Resolution of species ranges in the deep ocean requires a new scientific outlook. A combined molecular and morphological approach to evaluate species ranges would be highly valuable. Important conservation issues, such as predicting the impacts of manganese nodule mining, CO₂ disposal, iron fertilization and climate change require a better understanding of the diversity, life-history, species ranges and functional ecology of abyssal benthic fauna.

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