

# Appropriate levels of taxonomic discrimination in deep-sea studies: species vs family

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**ABSTRACT:** Few studies have investigated use of higher-level taxonomy, e.g. family, to analyse macrobenthic infaunal communities in the deep sea. This study uses multivariate analyses of polychaete macrofauna and environmental variables from 15 stations (depth 150 to 1000 m) situated in the Faroe-Shetland Channel (NE Atlantic). The data were analysed at species and family levels in order to determine the degree of taxonomic sufficiency required to discriminate between stations. There was little difference in results between species and family when using non-metric multi-dimensional scaling, however, cluster analysis and canonical correspondence analysis (CCA) showed marked differences between the 2 taxonomic levels. Similarity between stations was markedly lower at species than family level. The ability of CCA to separate the families into defined groups along the 2 ordination axes was more apparent than at species level. Families also tended to be more closely aggregated near the centre of the ordination plot. It is concluded that in the deep-sea, species-level identification of polychaetes is preferable to that of family-level identification.

**KEY WORDS:** Taxonomic discrimination · Species · Families · Deep-sea · Macrobenthos

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## INTRODUCTION

To identify major patterns in community structure, and to relate them to measured environmental variables, fauna have traditionally been identified to species level. Whether identification to species level or to a higher taxonomic level would suffice to detect faunal response to changes in the environment, particularly disturbance arising from pollution, has been the subject of considerable debate (e.g. Bayne et al. 1988, Warwick 1988a,b, Ferraro & Cole 1990, Gray et al. 1990). The traditional view has been that identification of fauna to a higher taxonomic level would not result in sufficient discrimination because differences in species-level responses may be masked between sites. However, identification to a higher taxonomic level, e.g. family, may be desirable in order to save time and/or money.

However, macro- and meiofaunal data collected from putative pollution gradients in Frierfjord and Langesundfjord, Norway, analysed by the community ecology group of the Group of Experts on the Effect of

Pollution (GEEP), found that results of data analysis using multivariate techniques are little affected by the aggregation of species data into higher taxonomic groups (Heip et al. 1988, Herman & Heip 1988, Warwick 1988a,b). Warwick (1988c) concluded that at higher taxonomic levels, little information regarding the effects of pollution gradients was lost, even at phylum level, although this does not hold true for meiofauna (Sommerfield & Clarke 1995). Ferraro & Cole (1990) reached a similar conclusion when assessing impacts of pollution on macrobenthos in the Southern California Bight, as did Gray et al. (1990) in studies undertaken in the Ekofisk and Eldfisk oil fields in the North Sea.

A higher faunal grouping, e.g. family, will normally include evolutionary adaptation to a broad range of environmental variables among species filling specific niches. Only subsets of the component species are likely to have adaptation allowing them to tolerate anthropogenic stressors.

Warwick (1988a) suggested possible advantages of identifying fauna to a level higher than species when

using multivariate analyses. Depth and sediment granulometry have been identified as 2 of the most important natural variables affecting the structure of the benthic community. By being more finely tuned to depth and sediment, species-level adaptation may obscure a response to a contaminant over a wider area, covering a range of depth and sediment types. These variables generally influence the fauna more by species replacement than by actual changes in the proportion of the major taxa present (Warwick 1988a). Warwick found that ordination plots of total individual abundance and biomass were more strongly correlated with a gradient in contamination than were species ordinations. Family-level analysis, however, may mask changes in species replacement, which would have relevance in any examination of disturbance.

Comparison of species-level with family-level uni- and multi-variate analyses has recently been undertaken by a few workers, e.g. Warwick (1988a), Gray et al. (1990) and Olsgard et al. (1997, 1998). In Warwick's re-analysis of studies of macrofauna in Loch Linnhe, the Clyde Sea and Bay of Morlaix, samples analysed to species level provided no extra information compared to family-level results (Warwick 1988c). At regularly monitored sites, Olsgard et al. (1998) argued that identification to family level and not species level might suffice. Olsgard et al. (1998) suggested that as disturbance increased in an area, faunal gradients would become stronger, and therefore identification of organisms to a higher taxonomic level would enable clearer taxonomic identification of community structures. However, for areas where little prior investigation has taken place, or for baseline studies, identification to species level is not only desirable but also necessary (Olsgard et al. 1998).

Ellis & Cross (1981) suggested that identification to a taxonomic level other than species was sometimes preferable, as species identification tends to be more error-prone as well as being more labour-intensive and expensive, and requiring considerable expertise. Statistically, and possibly biologically, it is more desirable to correctly identify fauna to a higher taxonomic level than incorrectly to species level (Green 1979). Aggregation of species to a higher taxonomic level appears to be useful if the aim is to investigate a major pollution gradient in the area. In the macrofauna, such taxonomic problems indicated above are often encountered with a number of polychaete families, e.g. Cirratulidae, Capitellidae and Spionidae (Warwick 1988c). Few studies have presented data where macrofauna are identified to a level higher than species, e.g. genera or family. It has been recommended that additional investigations comparing different taxonomic levels should be undertaken (Gray et al. 1990, Warwick et al. 1990, Vanderklift et al. 1996, Olsgard et al. 1997).

The debate on taxonomic sufficiency has so far concentrated on data collected from inshore and continental shelf areas; little comparative analysis has been undertaken in deeper water. The work undertaken in the present study aims to inform this debate from a deep-sea perspective. Here, species-level taxonomy has traditionally been applied to analysis of macrobenthic communities. To our knowledge there have been no investigations on the utility of higher-level taxonomy in order to discriminate communities in the deep-sea, particularly in response to environmental variability and anthropogenic impact.

The objective of this study, therefore, is to determine whether the same level of discrimination, or taxonomic sufficiency, can be achieved by identifying fauna to family level as opposed to species level along a depth transect from the shelf-edge to the deep-sea. Identification of deep-sea fauna to species level is often difficult, hence identification to family level may facilitate deep-sea studies should family level identification prove adequate. In the present study the Polychaeta are used as a proxy for the total community as used in other deep-sea community analysis (e.g. Glover et al. 2001). Stations along this depth gradient are known to encompass a wide range in environmental variability, such as changes in temperature and sediment grain size (Bett 2000, Narayanaswamy 2000).

## MATERIALS AND METHODS

**Background to study area.** The Faroe-Shetland Channel is situated between the Scottish continental shelf and Faroese Plateau. Five water masses flow and converge in the Channel, giving rise to a highly dynamic and unusual physical environment (Dooley & Meincke 1981, Hansen 1985, Turrell et al. 1999). Cold, dense Norwegian Sea water flows in a south-westerly direction and is overlain by warm saline North Atlantic water flowing towards the northeast along the eastern side of the Channel (Turrell et al. 1999). The boundary region between the warm- and cold-water masses occurring at a depth of 350 to 650 m (although this may vary) is of particular interest. A current meter located at a depth of 550 m, 10 mo prior to the present study, recorded temperature range varying dramatically (Bett 2000). On several occasions the temperature dropped 7°C in the space of 1 h, and each occurrence lasted for a period of 4 to 5 h (Bett 2000). Internal tides may be responsible for this rapid temperature change as they can cause intermediate waters to move vertically by as much as 100 m during a 6 h period (Bullough et al. 1998). The strong vertical gradient in environmental conditions associated with the structure of these water masses provides an unusual disturbance gradient against which to test our objective.

**Sampling methods.** A bathymetric transect consisting of 15 stations, ranging in depth from 150 to 1000 m, were sampled along the West Shetland Slope (Fig. 1) on RRS 'Charles Darwin' in July 1996 (Cruise 101C) and May–June 1998 (Cruise 112) (Bett 1997, 1999). The stations covered widely differing sediment types (see Bett 2000), and hence 3 different seabed samplers were employed; a Day grab (Holme & McIntyre 1984) for the depth range 150 to 300 m, an USNEL box corer (Hessler & Jumars 1974) for stations situated between 350 and 500 m, and a megacorer (cf. Barnett et al. 1984) for the remaining stations, 550 to 1000 m. The megacorer was found not to be an effective sampler in the shelf edge region of the Faroe-Shetland Channel (Bett & Gage 2000). A pair-wise comparison of the sampling gear to determine any sampler bias was undertaken on samples collected for the Atlantic Frontier Environmental Survey by Bett (2000). It was found that faunal composition did not exhibit any statistically significant difference when comparing the 3 seabed samplers (Bett 2000).

Macrobenthos was collected from 8 pooled megacore samples (0.063 m<sup>2</sup>), a 0.1 m<sup>2</sup> insert placed inside the box core, or the entire contents from a Day grab sample, in order to reach a volume of 5 l. Samples were sieved on 0.5 and 0.25 mm stacked sieves aboard ship and the residue immediately fixed in 4% buffered for-

malin. Prior to sorting, a solution of 1% Rose Bengal was added to aid in the removal of the macrofauna from the 0.5 mm fraction (excluding nematodes, ostracods and copepods). The polychaetes were sorted under a binocular microscope to the lowest possible taxonomic level, species or putative species level.

A suite of environmental variables was also measured: maximum and minimum temperature; mean sediment grain size; silt/clay fraction; total organic nitrogen/carbon, as well as aliphatic/aromatic hydrocarbons. Whilst an in-depth analysis of the environmental data is beyond the scope of this paper, details of the collection, analysis and results are given by Bett (1997, 1999, 2000).

Polychaete species abundance from each station was also aggregated to family level. Analysis of similarity (ANOSIM), cluster analysis and non-metric multidimensional scaling (MDS) using the PRIMER package (Clarke & Warwick 1994) and correspondence analysis (CA) and canonical correspondence analysis (CCA) from the CANOCO package (ter Braak & Smilauer 2002) were carried out at both taxonomic levels (species and family). Bray-Curtis similarity was used to construct a similarity matrix and a 4th-root transformation was applied. To classify the stations based on polychaete groupings, the similarity matrix was subject to hierarchical, agglomerative classification, em-

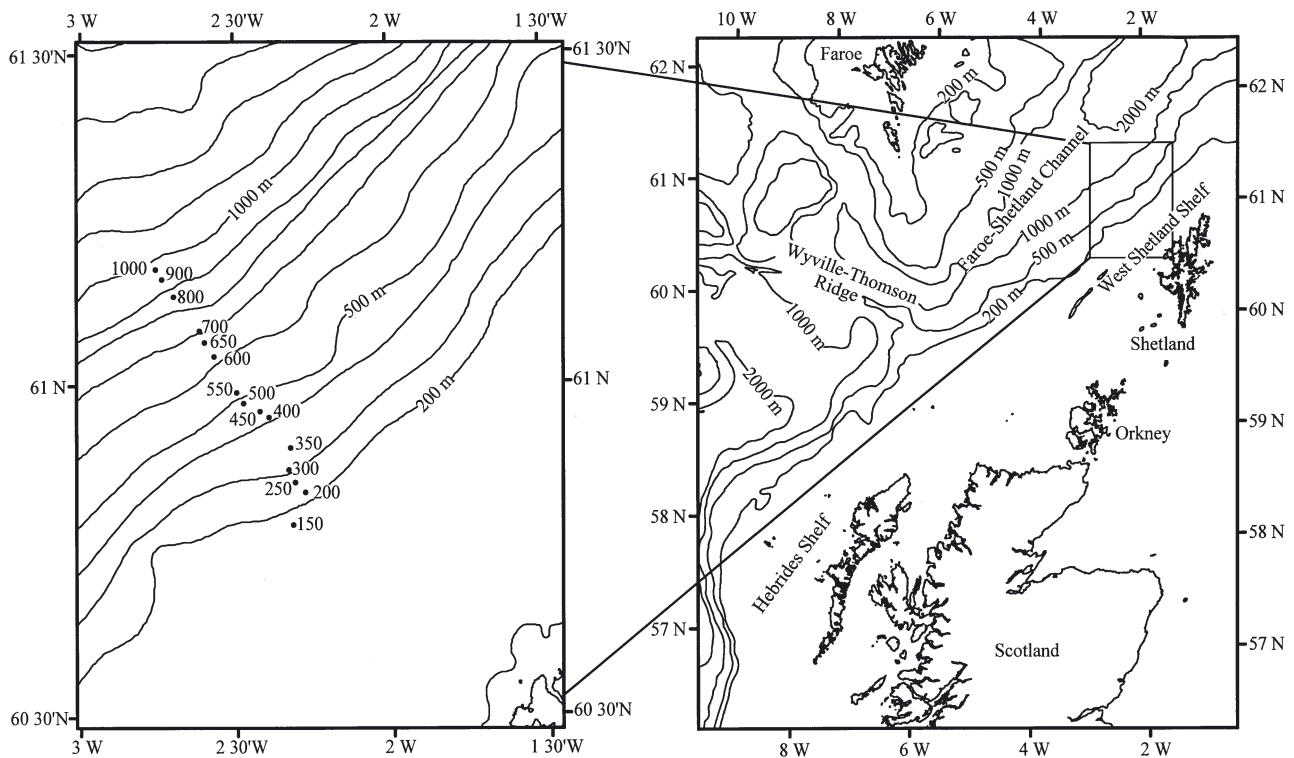


Fig. 1. Chart of the West Shetland Slope with inset showing the 15 transect stations (●)

ploying group-average sorting (Lance & Williams 1967). The matrix was used to plot hierarchical dendrograms and non-metric MDS ordinations (Shepard 1962, Kruskal 1964). The goodness-of-fit in the MDS ordinations were measured using Kruskal's stress formula (Kruskal & Wish 1978). CA and CCA were used to analyse the relationship between polychaete community structure and the suite of environmental variables measured. This method has been found useful and effective in evaluating the relationship between environmental variables and faunal composition (ter Braak 1987, Brown et al. 1992). Within CCA, forward selection was applied to remove depth from the analysis, as it was a co-variable. To test the statistical significance of the relationship between polychaetes and environmental variables, a Monte Carlo permutation test within CCA was used (Manly 1991, ter Braak 1992). This gives the significance of the first eigenvalue and the sum of the eigenvalues (ter Braak 1987). The eigenvalues presented measure the total amount of variance, whilst canonical eigenvalues measure the variance with respect to the environmental variables used (ter Braak & Smilauer 2002). Environmental variables were correlated with the ordination axes, using a partial Pearson correlation, where more than 1 environmental variable was significantly correlated with an axis.

## RESULTS

ANOSIM was used to determine whether using 3 different sampling gears influenced the results. Samples using the same gear in each year were combined as replicates within ANOSIM and run at each taxonomic level. At both species and family level there was found to be no significant difference ( $p < 0.1$ ) between the gears.

### Cluster analysis and non-metric multi-dimensional scaling

The following analyses were undertaken on data that was initially untransformed, followed by square- and 4th-root transformations as well as reduction to presence-absence. Although most of the ordination plots and stress values yielded similar results, 4th-root transformation was used to allow the mid-range and rarer species to exert some influence on the calculation of similarity (Clarke & Warwick 1994).

Cluster analysis (Fig. 2) shows that the percentage similarity between stations at species level is much lower (15 to 20%) than at family level (40 to 50%). All 4 plots show a clear separation of stations into a shallow group 150 to 500/600 m (species), 150 to 500/550 m

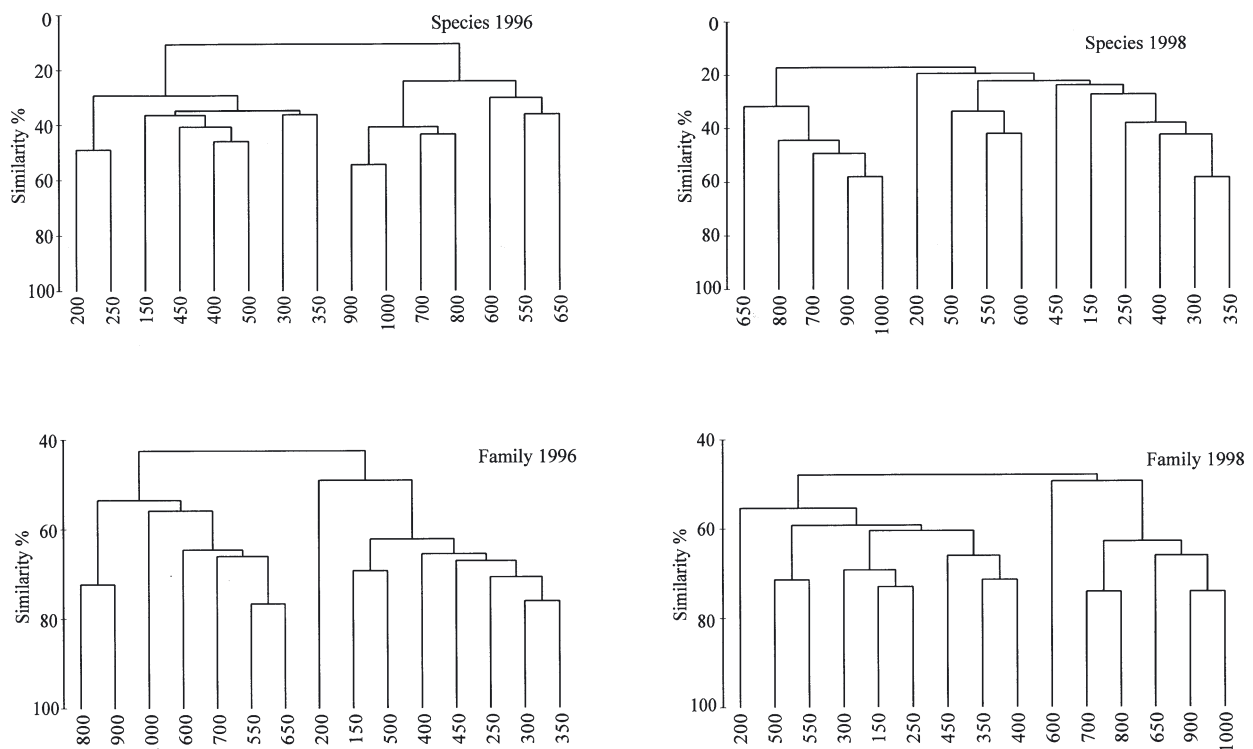


Fig. 2. Hierarchical dendrograms of Bray-Curtis similarities of polychaete species- and family-level taxonomy (numbers indicate station depth)

(family) and a deep group 550/650 to 1000 m (species), 550/600 to 1000 m (family). The 1998 species-level cluster plot shows some further degree of separation in the shallow grouping, forming an intermediate depth group (500 to 600 m).

The non-metric MDS ordination plots for the transect data (Fig. 3) show in all 4 ordination plots that separation between the shallow and deep stations is slightly more evident in the species-level plots than at family level. This suggests that as abundances are aggregated to higher taxonomic levels, the general patterns of the community structure are retained. The stress associated with the ordination plots is marginally lower at family level (0.1 in 1996, 0.12 in 1998) than species level (0.11 in 1996, 0.16 in 1998), indicating a better 2D representation of the data at family level.

**CCA**

Using both CA and CCA in both years and at both taxonomic levels, Axes 1 and 2 on the canonical ordination plots were the most important (Table 1). Only at species level were the first 2 axes' eigenvalues >0.5. Relatively good dispersal of the species along the different axes is thought to be denoted by eigenvalues which are >0.5 and, as ter Braak (1986) suggests, this would account for a large percentage of the variance in species composition. However, all 4 data sets indicate a high correlation between polychaete composition and the environmental variables on the first 4 axes (Table 1). This indicates that the environmental variables measured in this study account for most of the variance in the biological data. In total 10 environmental variables were measured, which accounted for between 62 and 71 % of the variability of the polychaete composition at both species and family level.

An unrestricted Monte Carlo permutation test was applied to the forward selection of the environmental variables. Each taxonomic level and year had 2 or 3 environmental variables, accounting for a significant proportion ( $p < 0.05$ ) of the variance seen at polychaete species and family level (Table 2). At species level, these variables accounted for between 56 and 41 % (1.61 eigenvalues out of 2.85 in 1996; 1.18 eigenvalues out of 2.88 in 1998) of the total variability, whilst at family level,

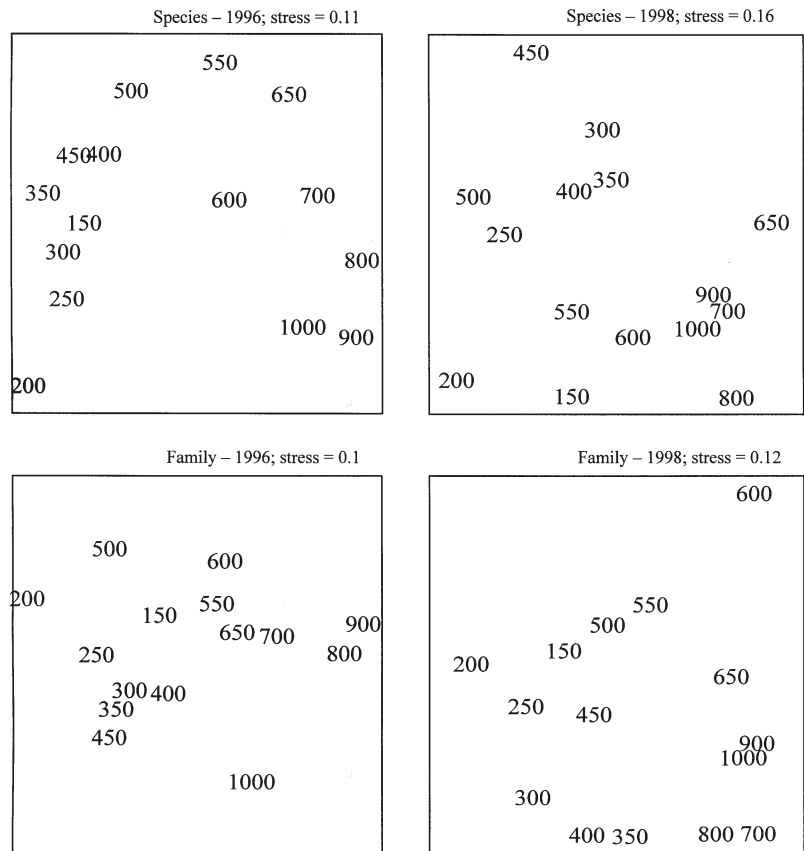


Fig. 3. Non-metric multi-dimensional scaling ordinations of polychaete species and family abundance (numbers indicate station depth)

Table 1. Results of correspondence analysis (CA) and canonical correspondence analysis (CCA) for polychaete species/families and environmental variables in 1996 and 1998. EC: environmental correlation

Analysis	Taxonomic level/year	Axes			
		1	2	3	4
CA	1996 - species				
	Eigenvalues	0.82	0.53	0.46	0.36
CCA	1996 - species				
	Eigenvalues	0.99	0.96	0.92	0.65
CA	1998 - species				
	Eigenvalues	0.82	0.51	0.45	0.34
CCA	1998 - species				
	Eigenvalues	0.99	0.99	0.99	0.99
CA	1996 - family				
	Eigenvalues	0.80	0.54	0.49	0.46
CCA	1996 - family				
	Eigenvalues	0.98	0.76	0.81	0.81
CA	1998 - family				
	Eigenvalues	0.78	0.45	0.43	0.38
CCA	1998 - family				
	Eigenvalues	0.99	0.98	0.98	0.95
CA	1996 - species				
	Eigenvalues	0.45	0.32	0.24	0.17
CCA	1996 - species				
	Eigenvalues	0.96	0.94	0.81	0.84
CA	1998 - species				
	Eigenvalues	0.42	0.26	0.19	0.12
CCA	1998 - species				
	Eigenvalues	0.97	0.95	0.96	0.95
CA	1996 - family				
	Eigenvalues	0.45	0.32	0.24	0.17
CCA	1996 - family				
	Eigenvalues	0.96	0.94	0.81	0.84
CA	1998 - family				
	Eigenvalues	0.41	0.26	0.15	0.12
CCA	1998 - family				
	Eigenvalues	0.98	0.84	0.89	0.54
CA	1996 - species				
	Eigenvalues	0.41	0.21	0.15	0.09
CCA	1996 - species				
	Eigenvalues	0.99	0.93	0.99	0.96





Table 2. Results of the Monte Carlo permutation test based on forward selection with 999 unrestricted permutations analysing the influence of the environmental variables on polychaete species/family abundance. Variance of environmental variable accepted at the  $\leq 0.05$  level. Min: minimum temperature; Max: maximum temperature; Sed: mean sediment grain size; Org: organic content

Taxonomic level/year	Unconstrained eigenvalue	Canonical eigenvalue	Variance of variable	Variable
Species 1996	4.35	2.85	0.80	Max
			0.43	Sed
			0.38	Min
Species 1998	4.67	2.88	0.74	Max
			0.44	Min
Family 1996	1.77	1.26	0.41	Max
			0.25	Sed
Family 1998	1.44	0.99	0.38	Sed
			0.19	Max
			0.12	Org

separates the shallow from deep and the 2 intermediate sets of stations into a shallow–intermediate group and an intermediate–deep group. Strongly associated with Axis 1 is maximum temperature and total organic carbon, whilst there is no environmental variable closely linked to Axis 2. At family level, the separation of stations along the 2 axes is not so well defined, particularly along Axis 2 (Fig. 4). Axis 2 appears not to separate the shallow stations from the shallow–intermediate stations and the deep stations from the intermediate–deep stations as clearly as at species level.

## DISCUSSION

Previous studies in taxonomic sufficiency have been undertaken in relatively shallow water areas and all have found that it is possible to use results from a higher taxonomic resolution, e.g. family, to determine the response of the benthic community to environmental/pollution gradients.

In the present study, hierarchical cluster analysis separated the stations into 2 main groups at both species and family level. However, the actual clustering of stations is different between the 2 taxonomic levels, and the level of percentage similarity between the 2 main station groupings was markedly different: 2.5 times higher at family level than at species level. This is not surprising as species within the same family may have very different responses to environmental stressors. For example, some species, e.g. *Prionospio* spp., may inhabit an area where the temperature range is quite high (~5 to 6°C), whilst other spionid species, e.g. *Spiophanes kroyeri*, appear to inhabit regions where the temperature range is quite low (<1°C). The results from the different species are aggregated into 1 family,

thus differences between families are not as noticeable as differences between species.

Furthermore, the level of stress imposed on the MDS ordinations was found to be only slightly lower at family than species level. Somerfield & Clarke (1995) also found that non-metric MDS ordination plots from higher taxonomic levels had lower stress values, and thus MDS preserves inter-sample relationships in 2D plots. Again this result is unsurprising as the number of polychaete families used in the analysis was 40 (1996) and 33 (1998), compared to 169 species (1996) and 147 species (1998). By collapsing the heterogeneity among species into family groups, adap-

tational characteristics are averaged so that response to environmental variables among families will appear more similar than among individual species.

Thus, the MDS results from this study appear to be similar to those undertaken in shallow water areas, comparing the discriminatory ability of higher-level taxa with species level. Somerfield & Clarke (1995) found that in Liverpool Bay and the Fal Estuary, there were no striking differences between species and genus abundances at the 2 study sites, although at levels higher than genus, ANOSIM was less able to discriminate between the stations. Ferraro & Cole (1990) obtained similar results when comparing species with order level in the Southern California Bight, as did Olsgard et al. (1997) in the Valhall oil and gas fields. Their results also support those of Heip et al. (1988), Warwick (1988a,b) and Kingston & Riddle (1989).

In all CCA ordinations (Fig. 4), the shallowest stations and generally the species/family that occur at these depths are closely associated with the temperature eigenvectors, indicating that they are able to tolerate higher water temperatures. At species level, intermediate depth stations and species that are more common at these depths are strongly linked to the temperature range, suggesting they are able to tolerate large variations in temperature. Conversely, species at the deeper stations appear not to be able to withstand such great changes in temperature and therefore tend to lie on the inverse of temperature range. At family level, sediment grain size and organic matter are associated with the families prominent at the deeper stations, implying that these families are strongly influenced by finer grained sediments and the quantity of organic material present.

When using CCA ordinations however, it is more difficult to compare immediately any similarities or dif-

ferences in the positioning of species and families. On both sets of ordination plots at the 2 taxonomic levels, there is a clear separation between shallow, intermediate and deep stations, although separation of families along Axes 1 and 2 is not as clear compared to species. It is more difficult to place families on the ordination plots, as different species within each family may have a close affinity with different environmental variables. This may result in some families being located closer to the centre of the ordination plots. In the example given previously, this may be as a result of *Spiophanes kroyeri* having a greater number of individuals per species than for all of the *Prionospio* species put together. Therefore, the family Spionidae is located more towards the centre of the ordination plots, although somewhat closer to the environmental variables associated with *S. kroyeri*. However, some species that dominate in a particular depth band and are associated with particular variables appear to belong to families that show a similar concomitance, e.g. *Glyceria lapidum* complex is strongly affiliated with the temperature variables, an association which is also seen in the family Glyceridae.

The range of environmental tolerance within a major taxonomic group is the sum of differing adaptation shown by individual species. It follows that few of these species will have tolerance to stress such as that caused by pollution (Warwick 1988c). Thus, the abundance and biomass of major taxa is more likely than individual species to show correlation to a pollution gradient. Olsgard et al. (1998) suggest that if a gradient in environment or pollution reduces the number of species in each family to a single species, then analysis of these samples could be undertaken at family level, as the outcome would be identical to that of the species-level analysis.

The presence of fewer polychaete families suggests that variability between the different polychaete families is more easily explained by the environmental variables measured. Increased numbers of species leads to potentially greater variability between the species, therefore other environmental variables, not measured here, may account for a high proportion of the variability. The environmental variables measured that have a significant effect on polychaete composition in this study overall account for a higher proportion of the variability at family than species level.

Olsgard et al. (1998) correlated a suite of environmental variables with all the taxonomic levels from species to family at 3 oil and gas sites: Valhall, Gyda and Veselefrikk in the North Sea and known to have strong pollution gradients, over a number of years. They found that there was no simple relationship between the duration and intensity of pollution. Olsgard et al. (1998) found that areas with a longer pollution

history generally showed stronger correlations at a higher taxonomic level. There was little decrease in correlation between environmental variables and species and family.

In the present study, results at species level were similar to those obtained at family level when using MDS ordination. However, results from hierarchical cluster analysis and CCA ordination indicates that similarity between the 2 taxonomic levels is reduced. The percentage similarity between stations was much lower at species level, probably a reflection of the varying responses of the species to the environmental variables measured. Species-level analysis also appeared to be more sensitive in separating species along the 2 ordination axes in CCA. Species-level analysis also indicated that other environmental variables not measured in this study might account for a higher proportion of the variability at species level. At family level, it is more difficult to discriminate between the stations. This is probably a result of species within the same family exhibiting widely differing relationships with the environmental variables measured.

A comparison of the 1996 and 1998 family results does show some similar trends to 1996 and 1998 species results. Hierarchical cluster analysis separates the stations into 2 main groups at both levels and years. The differences in station clustering at species level are similar to those at family level. The 200 m station appears to be quite distinct at family level; however, this is only reflected in 1998 at species level. The 600 m station appears to be quite different in 1998 at family level, showing a relatively low similarity; however, this is not seen in the 1996 family or species level or at the 1998 species level. Similar patterns occur using non-metric MDS ordinations whereby differences between years at one taxonomic level are not necessarily reflected in the other taxonomic level studied. Trends in the CCA ordination plots are less apparent as comparisons are between the placement of species on the ordination plot with families on ordination plots.

In many macrobenthic studies, identification of fauna to species level is not only time-consuming, but also expensive. Ferraro et al. (1989) found that abundance counts and species identification accounted for 60% of the laboratory processing time. Olsgard et al. (1998) determined from their investigations that by aggregating their data from species to family level, the mean number of taxa was reduced by 54.5%, which in turn indicated a saving of approximately 50%. In this present study, aggregation to family from species level reduced the average number of taxa by 61 to 64%, suggesting that more than 50% of the cost (based on Olsgard et al.'s 1998 figures) could have been saved had identification only been conducted to family level.



When the above findings are taken into consideration, together with the paucity of previous work from the region, we conclude that for the purpose of detecting change from a baseline in a relatively poorly known bathyal province, identification of polychaetes to species level remains preferable to family level.

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