

Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean

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ABSTRACT: Diversity and structure of copepod assemblages were investigated using 259 WP2 zooplankton samples collected from the top 200 m of the Atlantic Ocean between 60°N and 63°S. Whilst richness at a number of taxonomic levels (genera-superfamily) demonstrated a smooth latitudinal cline from the tropics towards the poles, other diversity indices such as evenness and taxonomic distinctness showed abrupt changes around 40°N and 40°S, coincident with sea surface temperatures of 17 to 20°C. In the tropics and subtropics, copepod communities were characterised by high stable taxonomic diversity and a relatively even distribution of genera within samples. In contrast, at high latitudes and low temperatures communities showed large variation in overall diversity, evenness and distinctness. Multidimensional scaling and cluster analysis of transformed generic abundances, pooled into 5° latitudinal means, produced ordinations consistent with the recent subdivision of the oceans into 4 primary biomes based on temporal and spatial patterns of primary production. The copepod community corresponding to the Trades biome, where primary production is broadly continuous, exhibited high generic richness and evenness. In contrast, community structure in the Polar biome, where primary production is highly seasonal, was highly variable and dominated by a few genera. These genera tended to be herbivorous or omnivorous and stored lipid. The Westerlies biome and the Benguela province had intermediate copepod community characteristics. We therefore suggest that copepod diversity and community structure are closely tied not to temperature or energy input, but to the temporal patterns of primary and secondary production.

KEY WORDS: Copepoda · Diversity · Community structure · Latitudinal gradient · Atlantic Ocean

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INTRODUCTION

In recent years there has been a resurgence of interest in marine diversity, both in documenting the large-scale patterns and also in determining the underlying processes which produce these. As Angel (1993, 1997) has emphasised, early attempts to understand the biogeographic patterns evident in zooplankton distribution were hindered by the apparent lack of stable structure in the ocean that might create such patterns. The classical approach of marine biogeography has been to map provincial and regional patterns of spe-

cies distribution in a largely qualitative way. This has established a generally accepted 9 belt zonal system which is strongly coincident with watermass boundaries (Boltovskoy 1998). This pattern of zooplankton distribution is largely controlled by a small number of numerically dominant species rather than the large number of scarcer taxa (McGowan 1986, Boltovskoy 1998). Whilst providing a wealth of information on species distributions, this approach has fallen some way short of providing us with a functional ecology of the pelagic realm.

Using a fundamentally different approach, Longhurst (1998) has recently established the framework for a global regional ecology of the marine environment

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based on a suite of physical processes in conjunction with what we know about the seasonal response of phytoplankton to such processes. Using this mixture of physical and biological criteria, he divided each of the world's ocean basins into 4 major regions: Trades, Westerlies, Polar and Coastal biomes. These can themselves be further subdivided into a total of 51 biogeochemical provinces. For each of these provinces it is possible to follow the seasonal evolution of phytoplankton biomass and to relate this to rates of production and loss. A recent attempt to establish congruence between Longhurst's biogeochemical provinces and biogeographic patterns, and thereby provide support for the division of the ocean into functionally distinct provinces, was made by Gibbons (1997). His analysis of euphausiid distributions in the South Atlantic, based on simple presence or absence of different species, was in basic agreement with the earlier biogeographic divisions of van der Spoel & Heyman (1983), but provided only partial support for the partitioning at the biogeochemical level proposed by Longhurst (1998). This may have been a result of a qualitative (presence/absence) approach as many of the euphausiids in this region have widespread distributions. Boltovskoy (1998) has suggested that the advent of a more quantitative approach to classical biogeography has yet to alter significantly our perception of the major divisions in the world ocean. The increasing recognition of taxonomic uncertainties and lack of large-scale distributional data sets have significantly hindered progress.

While these traditional methods have provided us with a broad view of plankton diversity, the relative lack of large-scale distributional data has not allowed patterns to be examined systematically on a global scale. We know that communities in the oligotrophic tropical regions typically contain more species than their polar counterparts, and also that the distribution of many taxa exhibits a latitudinal cline (e.g. Bé 1977, Angel 1997). For some groups, however, such as euphausiids, pteropods and chaetognaths, species richness is greatest in middle latitudes (Boltovskoy et al. 1999).

Latitude in itself does not directly determine richness or biodiversity, but is a covariate of a number of potentially causal environmental factors (Gaston 2000). One such factor is sea temperature, which has been shown to be strongly correlated with diversity in some plankton groups (e.g. Rutherford et al. 1999) and can be an indicator of community structure (e.g. Gibbons 1997). A number of other hypotheses have been proposed to explain geographic variation in species richness including surface area of provinces (Rosenzweig 1995), environmental stability (Sanders 1969), energy input (Wright 1983), evolutionary history (Crame & Clarke 1997) and gradients in physical environmental proper-

ties (Rohde 1992, Gaston 2000). Several of these have been examined in respect to zooplankton. Energy input into zooplankton communities can be estimated from phytoplankton standing stock or primary production. Theory suggests that high energy input may be associated with high diversity (Cousins 1989). However, high productivity levels are found in the Polar regions (Longhurst et al. 1995), where zooplankton diversity is typically low. Diversity does not closely match changes in area of the different regions of the ocean either (Longhurst et al. 1995, Rutherford et al. 1999), and pelagic diversity is low at both poles despite the very different evolutionary history of the Arctic and Antarctic. Current data thus suggest that there is no single or simple explanation for global patterns of zooplankton richness.

Simple taxonomic richness is only 1 aspect of community function, and the balance of functional types is also critical. An approach taken by Longhurst (1998) was to aggregate within higher taxonomic categories the biota occurring in each of his 4 biomes. This analysis suggests that there are important functional differences between them with major shifts in many of the abundant taxa between tropics and poles allied to changes in trophic grouping. For example, raptorial zooplankton predators increased from between 19% (Arctic) and 24% carbon biomass (Antarctic) in the Polar biome, to 29% in the Atlantic Trades, whereas macro-herbivores fell from between 48 and 65% to 22% over the same biomes. Despite these striking large-scale shifts in functional groups of zooplankton, we remain largely ignorant of the way these communities are regulated.

We have therefore analysed a series of zooplankton samples taken along transects in the Atlantic Ocean spanning 60°N to 63°S. We have examined patterns of distribution, abundance and diversity within the Copepoda, and assessed how these relate to the ecological partitions made by Longhurst (1998). Copepods are abundant, generally dominating mesozooplankton assemblages both in terms of abundance and biomass and are important in the transfer of carbon within the world's oceans, and as food for higher predators. Because they are trophically diverse, the balance and relative importance of different groups should reflect major changes in underlying patterns of production in the upper water column.

MATERIALS AND METHODS

Sampling strategy. The samples used in this study were collected in the Atlantic Ocean during 7 cruises (Table 1, Fig. 1). All samples were taken with WP2 (200 µm mesh) nets deployed from 200 m to the sur-

Table 1. Summary of cruises and sampling. Dates are given dd/mm/yy

Cruise	Start date	End date	No. of samples	Lat. range
JR 11	04/01/96	10/01/96	21	48°S–53°S
JR 17	16/12/96	23/12/96	21	48°S–53°S
JR 28	17/01/98	21/01/98	21	48°S–53°S
JR 38	20/12/98	25/12/98	22	48°S–53°S
JR 47	12/01/00	15/02/00	25	52°S–63°S
PRIME	11/06/96	23/07/96	34	59°N & 37°N
AMT 4	21/04/97	27/05/97	41	50°N–50°S
AMT 5	15/09/97	17/10/97	38	50°N–50°S
AMT 6	14/05/98	16/06/98	36	50°N–35°S
Total			259	59°N–63°S

face, and the samples preserved with borax-buffered formalin (4%) for subsequent taxonomic identification. Sea surface temperature (SST) was collected simultaneously with the samples using the ship's thermosalinograph (Sea-Bird Electronics) to measure seawater pumped from approximately 6 m.

Genus was chosen as the most appropriate level of taxonomic resolution for copepods. Identification to species level was not undertaken because of unreliable taxonomy within this diverse group over such a large latitudinal range and the difficulties of identifying sub-adult stages. Use of higher taxonomic levels is not uncommon in diversity studies and has been shown to be highly correlated with species richness for a wide range of organisms (Williams & Gaston 1994, Williams et al. 1994, Roy et al. 1996). Moreover, in some cases trends are clearer at the generic level than at species level for analyses over large spatial scales (Roy et al. 1996). Analyses of community structure have also shown that the use of higher taxa does not substantially alter the patterns (James et al. 1995, Somerfield & Clarke 1995, Olsford et al. 1997).

For AMT and PRIME samples (Table 1), copepod genera were identified within the 4 Joint Global Ocean Flux Study (JGOFS) size classes (200–500, 500–1000, 1000–2000 and >2000 μm) following sieve fractionation. A sub-sample was taken from a known volume using a Stempel pipette, and a minimum of 200 copepods were identified. Where the number of copepods was less than 200 in that size fraction, the complete size fraction was counted. The southern polar samples were subdivided with a Folsom plankton splitter into various aliquots to reflect the different size spectra of copepods in each sample. The object being again to count a minimum of 200 animals in each fraction. A mean number of 848 copepods (interquartile range 615 to 990) was counted per sample. Abundance (m^{-3}) was calculated, assuming 100% filtration efficiency. Small calanoid copepods such as *Paracalanus*, *Pseudo-*

calanus and *Clausocalanus* were not distinguished, and were grouped as 'small calanoids'.

Biases within the data set. Due to the net mesh used (200 μm), smaller genera and young copepodite stages were likely to be under-sampled (Gallienne & Robins 2001, Hopcroft et al. 2001), and absolute diversity to be under-estimated. However, the treatment consistent, so patterns should not have been affected.

Because samples came from the top 200 m, only epipelagic zooplankton have been considered here. The deeper community will contain other genera which may inhabit surface waters at seasons or times of day that were not sampled. However, seasonal effects are most likely at high latitudes, and here sampling was undertaken during the productive summer months when most surface genera are present in the surface waters sampled. Diel effects are most likely to have reduced the numbers of genera sampled at lower

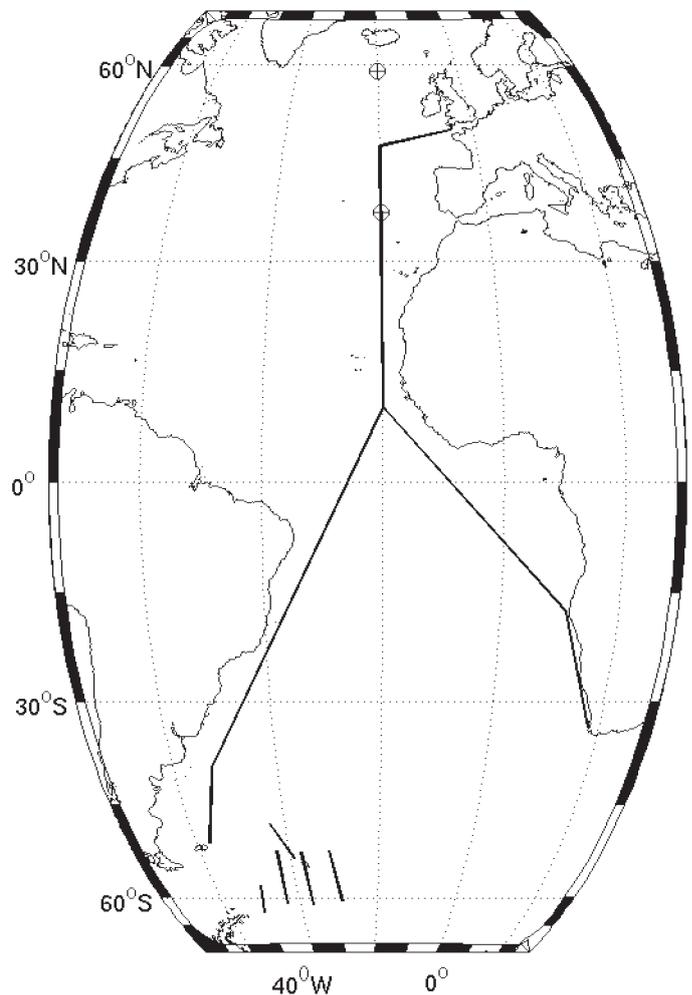


Fig. 1. Map of the Atlantic Ocean showing ship tracks for JR and AMT cruises, and sampling positions for the PRIME cruise. Details of the cruises are given in Table 1

latitudes, where most samples were taken during the day. Night samples tended to have higher generic richness, but not significantly ($F = 3.64$, $p = 0.06$). Comparisons of the overall community structure (Bray-Curtis similarity), however, did not show any major differences between day and night sampling, suggesting the impact of the different biomes was much larger than any diel effects (also see Woodd-Walker 2001). In terms of community composition, the northern polar region is the most likely to be biased, as data are available from just 1 station on a single cruise.

Because differences in sampling and analysis protocols can influence results, these biases were tested. There was no indication that the number of copepods counted or that the person identifying them affected the number of genera determined. Where there was

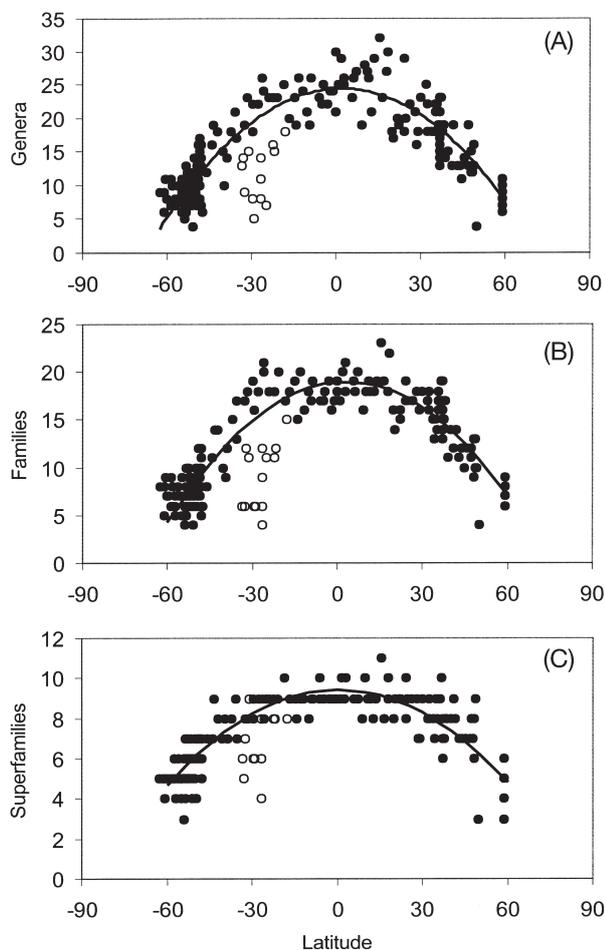


Fig. 2. Large-scale spatial variation in taxonomic richness of epipelagic copepod assemblages from the Atlantic Ocean. (A) copepod genera, (B) families, (C) superfamilies. Data for each sample are plotted individually (●); data for the Benguela upwelling region are plotted separately (○), and excluded from statistical analyses. Also shown are second-order polynomial statistical models (statistical data shown in Table 3). By convention latitudes S are shown negative

latitudinal overlap between the different sampling and analysis regimes, the results did not differ significantly (ANOVA, $F = 1.63$, $p = 0.20$). The number of genera in each sample was found to be unrelated to the number of individuals counted (General Linear Model, GLM, $F = 2.18$, $p = 0.14$), although when samples were pooled into 5° latitudinal bands, there was a significant effect (GLM, $F = 2.81$, $p = 0.011$) due to 2 bins with very large numbers of samples (at 55° S with 67 samples and 35° N with 26 samples) and slightly more genera were detected compared to adjacent bands. However, this effect was small compared to that of latitude (GLM, $F = 68.5$, $p < 0.001$).

Univariate analysis. Biodiversity is a multifaceted concept and can be considered to have 3 major components: the number of taxa (richness), the distribution of abundance within taxa (evenness) and the relatedness of different taxa (distinctness) (Purvis & Hector 2000). Recently Warwick & Clarke (1995) developed an index of taxonomic diversity, delta (Δ), which includes all 3 aspects of diversity. It is based on Simpson's index with an additional distinctness component. This was calculated as follows to give an overall measure of diversity:

$$\Delta = \frac{\sum \sum_{i < j} w_{ij} x_i x_j + \sum_i 0. x_i (x_i - 1) / 2}{\sum \sum_{i < j} x_i x_j + \sum_i x_i (x_i - 1) / 2}$$

where x_i is the abundance of the i th species and w_{ij} is the distinctness weight linking species or genera, in this case i and j . For this analysis, taxa in the same genera were weighted as 1, family as 2, superfamily as 3, and class as 4.

Individual components of diversity were also calculated. Richness was represented by the numbers of genera, subfamilies and families per sample. Sample evenness was calculated using Pielou's (1975) evenness J' .

$$H' = -\sum p_i \ln p_i$$

$$J' = H' (\text{obs}) / \ln S$$

where H' is the Shannon-Wiener diversity index, p_i is the proportion of the i th taxa and S is the number of taxa in the sample.

In the absence of a genetic phylogeny, the published morphological phylogenetic tree for copepods (Mauchline 1998, Bradford-Grieve et al. 1999) was used to calculate Clarke & Warwick's (1998) measure of taxonomic distinctness (Δ^+).

$$\Delta^+ = \frac{\sum \sum_{i < j} \omega_{ij}}{s(s-1)/2}$$

where s is the number of genera present, the double summation is over $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$ and ω_{ij} is the 'distinctness weight' between genera i and j . The same weightings were used as for taxonomic diversity (Δ).

Multivariate analysis. Preliminary inspection of the data suggested that community structure was not uniform across the sample set. Biogeographic patterns were therefore investigated using cluster analysis and non-metric multi-dimensional scaling (nMDS) within the software package PRIMER 5 (PRIMER-E Ltd 2000). The abundance data of the copepod genera were pooled into 5° latitudinal bins to reduce the number of samples, and were then double square root transformed to decrease the importance of dominant groups. Bray-Curtis similarities were calculated and cluster analysis carried out using group average similarities. Cluster analysis shows the similarity between samples and groups of samples as a dendrogram, and will form groups whatever the pattern of relatedness, whereas MDS displays the relative similarity between samples as the distance between points in low dimensional space. Thus tightly grouped samples are very similar, whereas more dispersed samples are more different, thereby providing a better visual representation of gradual changes than cluster analysis. The stress is a measure of the quality of the representation: low stress (<0.1) suggesting that the representation is good and high stress (>0.2) implying that care should be taken in interpretation (Clarke & Warwick 1994). Consistency between the results of clustering and MDS suggests robustness in the analysis. Analysis of similarity (ANOSIM in PRIMER5) was carried out on the individual samples to test the significance of the groups derived from the 5° bins. As with the pooled data, these were double root transformed before calculating the Bray-Curtis similarity coefficient, and 10 000 permutations were used to test the significance.

RESULTS

Diversity

Representatives of 47 genera of copepods from 25 families and 8 superfamilies were found in the 259 samples that were analysed (Table 2). Calanoid copepods dominated generic richness, and throughout most of the study area, small calanoids, together with *Oithona* spp. and *Oncaea* spp. were numerically dominant. The number of genera per sample showed considerable variation across the study area, with highest richness occurring in the tropics (Fig. 2A). Higher taxa (family and superfamily) showed a similar trend although the pattern was less pronounced at increasing taxonomic level (Fig. 2B,C). A second-order polynomial described the genera richness of the oceanic stations well (Table 3). Analysis of the residuals showed that variance in richness was approximately constant over latitude. The samples taken from the

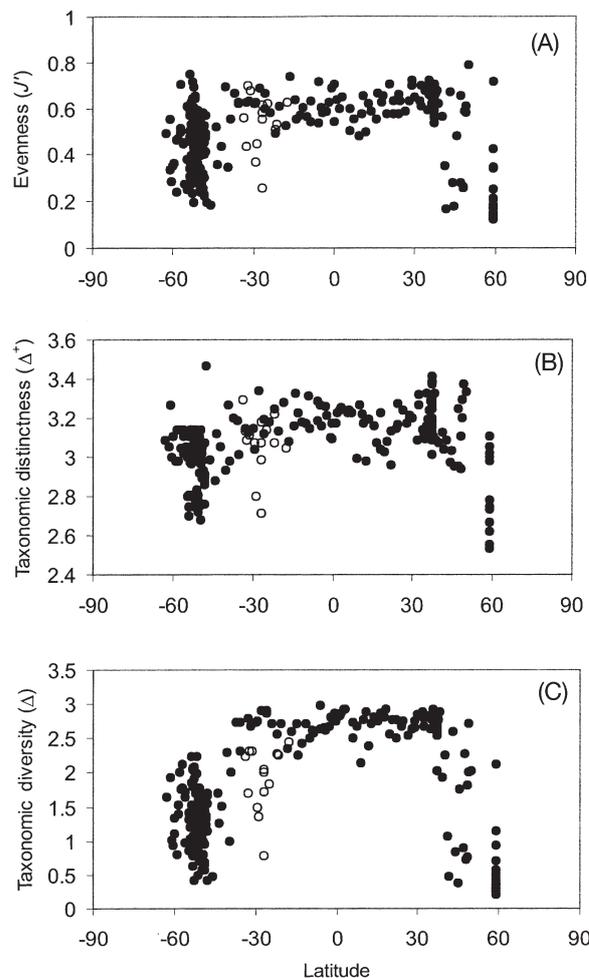


Fig. 3. Large-scale spatial variation in evenness and taxonomic distinctness of epipelagic copepod assemblages from the Atlantic Ocean. (A) Evenness (Pielou's J'), (B) taxonomic distinctness (Clarke & Warwick's Δ^*), (C) taxonomic diversity (Clarke & Warwick's Δ). Data for each sample plotted individually (●); data for the Benguela upwelling region are plotted separately (○), and excluded from statistical analyses. By convention latitudes S are shown negative

Benguela upwelling region were noticeably less diverse than those taken from the open ocean at similar latitudes, and were excluded from the statistical description.

There were also striking large-scale patterns in evenness and taxonomic distinctness (Fig. 3). Evenness was broadly similar in all samples between 40°N and 40°S; the mean value for oceanic stations was 0.62 and the variability relatively low (range 0.35 to 0.74), although once again the Benguela samples were distinct. At latitudes above about 40° both north and south, there was a striking increase in the variability of evenness (range 0.12 to 0.79) and an associated drop in

Table 2 (continued)

Biome	S. Polar 62.6°S–47.5°S	N. Polar 59°N	Westerlies 47.5–37.5°S, 42.5–50°N	Trades 37.5°S–42.5°N	Equatorial 7.5°S–17.5°N	Benguela 35°S–17.7°S	Overall 62.6°S–59°N
Latitudinal range							
No. of samples	113	18	19	95	22	14	259
Mean abundance (m ⁻³)	1103.96 (%)	1415.31 (%)	630.53 (%)	227.70 (%)	256.15 (%)	754.15 (%)	461.77 (%)
Megacalanoidae							
<i>Calanoides</i>	O ^a 19.53 (1.77)	0.07 (<0.01)	0.80 (0.13)	0.10 (0.04)	0.22 (0.08)	53.66 (7.12)	12.30 (2.66)
<i>Calanus</i>	O ^a 98.65 (8.94)	97.72 (6.90)	56.12 (8.90)	7.97 (3.50)	13.55 (5.29)	3.52 (0.47)	21.02 (4.55)
<i>Undinula</i>	4.10 (0.37)	–	<0.01 (<0.01)	0.60 (0.26)	1.87 (0.73)	0.00 (0.00)	0.66 (0.14)
<i>Calocalanus</i>	0.66 (0.06)	–	0.98 (0.16)	3.60 (1.58)	0.47 (0.18)	0.43 (0.06)	1.22 (0.27)
Small calanoids	O ^a 191.22 (17.32)	16.84 (1.89)	316.48 (50.19)	109.38 (48.03)	97.76 (38.16)	274.01 (36.33)	150.20 (32.53)
Cyclopoida							
<i>Oithona</i>	O ^f 617.95 (55.98)	1275 (90.04)	167.47 (26.56)	32.49 (14.27)	34.94 (13.64)	242.60 (32.17)	148.49 (32.16)
Harpacticoida							
<i>Cervinoidea</i>	–	–	–	0.05 (0.02)	0.02 (0.01)	–	0.03 (0.01)
<i>Clyemnestridae</i>	0.02 (<0.01)	–	0.36 (0.06)	0.09 (0.04)	0.17 (0.07)	–	0.09 (0.02)
<i>Miracidae</i>	–	0.91 (0.06)	0.24 (0.04)	0.73 (0.32)	1.92 (0.75)	0.10 (0.01)	0.55 (0.12)
<i>Miracia</i>	–	–	–	0.02 (0.01)	0.07 (0.03)	–	0.02 (<0.01)
Poecilostomatidae							
<i>Corycaeus</i>	–	–	6.21 (0.98)	11.64 (5.11)	14.45 (5.64)	0.60 (0.08)	7.39 (1.60)
<i>Lubbockia</i>	–	–	–	0.10 (0.04)	0.07 (0.03)	–	0.04 (0.01)
<i>Pachos</i>	–	–	–	0.01 (<0.01)	0.01 (<0.01)	–	<0.01 (<0.01)
<i>Oncaea</i>	O ^b 20.68 (1.87)	4.93 (0.35)	23.21 (3.68)	35.14 (15.43)	58.48 (22.83)	12.03 (1.59)	27.46 (5.95)
<i>Copilia</i>	–	–	–	0.09 (0.04)	0.12 (0.05)	–	0.05 (0.01)
<i>Sapphirina</i>	–	–	–	0.39 (0.17)	0.54 (0.21)	–	0.18 (0.04)
No. of genera	27	16	33	46	43	26	47

^aMauchline (1998), ^bPaffenhofer (1993), ^cTurner et al. (1984), ^dGophen & Harris (1981), ^eBradford et al. (1999), ^fAtkinson (1998)

the mean values to 0.41 (Fig. 3A). This change in evenness was related to a change in the abundance structure. At high latitudes (>50°N & S), *Oithona* tended to dominate, making up 90% of the total number of copepods (Table 2). Taxonomic distinctness (Δ^+) also showed a higher variance and lower mean at high latitudes (Fig. 3B). This may be caused in part by an overall reduction in the number of taxa, which can reduce the reliability of the estimates (Clarke & Warwick 1998). As with evenness, there was a wide band of broadly stable high values between 40°N and 40°S, and the Benguela data were also different.

When these 3 components of diversity (generic richness, evenness and taxonomic distinctness) were combined to produce a single taxonomic diversity index (Δ), there was a striking large-scale spatial pattern (Fig. 3C). At low latitudes, i.e. in the tropics, the taxonomic diversity is high with low variance. At latitudes greater than ~40°N & S, diversity is reduced and is highly variable. The diversity of samples taken from the Benguela upwelling region (35 to 17°S) were more similar to high latitude samples than those taken at similar latitudes, but away from upwelling regions.

Sea surface temperature

The strong patterns evident in the various diversity indices (Figs. 2 & 3) suggest an association with temperature: sea surface temperature is highly correlated with latitude in the open ocean and is also reduced in upwelling systems. A comparison of taxonomic diversity with temperature (Fig. 4) suggests a transition in community structure between 17 and 20°C, from high and stable diversity at temperatures above ~20°C, to lower and highly variable diversity below ~17°C. Comparing the number of genera with the evenness, for cold (<17.5°C) and warm waters (>17.5°C; Fig. 4B) also demonstrates a change in the community structure from predominantly cold

Table 3. Summary of statistical relationships of diversity indices with latitude for oceanic stations (excluding the Benguela). $p < 0.001$ for all R^2

Index	Intercept	x coefficient	x ² coefficient	R ²
No. of genera	24.41	0.00199	-0.0050	0.815
No. of families	18.96	0.0224	-0.0037	0.841
No. of superfamilies	9.42	0.0012	-0.0013	0.756

water samples with low numbers of genera and highly variable evenness to warm water samples with high evenness and high numbers of genera. Because the evenness of the warm and cold water assemblages within those areas is unrelated to the number of genera, it suggests that increase in the variance is not caused by the reduction in richness.

These plots, although exhibiting considerable variability, emphasise 2 important points. The first is that

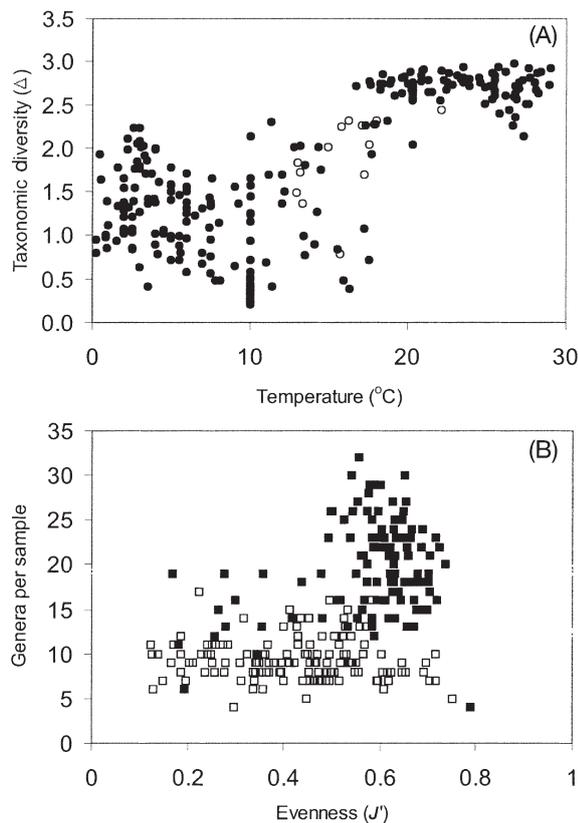


Fig. 4. (A) Relationship between taxonomic diversity (Δ) and sea-surface temperature (SST) for epipelagic copepod assemblages from the Atlantic Ocean. Data for each sample plotted individually (●); data for the Benguela upwelling region are plotted separately (○), and excluded from statistical analyses. (B) Relationship between generic richness and evenness (Pielou's J') for cold ($<17.5^\circ\text{C}$, □) and warm ($>17.5^\circ\text{C}$, ■)

there is no simple relationship between copepod diversity and temperature. The second is that something fundamental differs in community structure between copepods in warmer and colder water. That temperature is involved is suggested by the way the Benguela data fall within the general temperature relationship, whereas they fall separately as a function of latitude (Figs. 2 & 3). The relationship remains an association, however, for without an ecological mechanism to explain the underlying process, it may well be that SST is simply a strong proxy for whatever environmental factor(s) are actually regulating copepod diversity.

Multivariate analyses

The univariate analyses indicated strong spatial patterns in all the diversity indices calculated for the copepod data. We therefore used a number of multivariate analyses to determine the extent to which different samples clustered geographically/spatially. To do so, we utilised data pooled by bins of 5° of latitude in order to make the analyses more tractable and to reduce the variance. Both the cluster analysis and the MDS plots of copepod genera revealed a strong and consistent pattern for the 5° bins (Figs. 5 & 6). Community structure was found to be highly similar between 35°S and 40°N with both MDS and cluster analysis indicating a strongly related group of samples ($>80\%$ similarity). Within this grouping an equatorial sub-region was also apparent extending from 5°S to 15°N . Another cluster of slightly less closely related samples defined the mid-latitudes (40 to 45°S , 45 to 50°N), with increasing unrelatedness for the more polewards and polar groupings. The Benguela samples appear to form a distinct community, being somewhat similar to the mid-latitudes in taxonomic structure. Analysis was also undertaken at higher taxonomic levels (families and superfamilies) and this revealed a very similar clustering, suggesting that these changes in community structure are profound (data not shown).

Correlation with Longhurst's biomes

The major groupings that were identified in the sample set were highly consistent with the areas defined by Longhurst (1998) as the major biomes of the Atlantic Ocean. We therefore grouped the samples according to Longhurst's biomes and used ANOSIM to test for statistical similarities in assemblage composition between them. This analysis used individual sample Bray-Curtis similarities derived from double-root transformed genera abundances, and indicated that

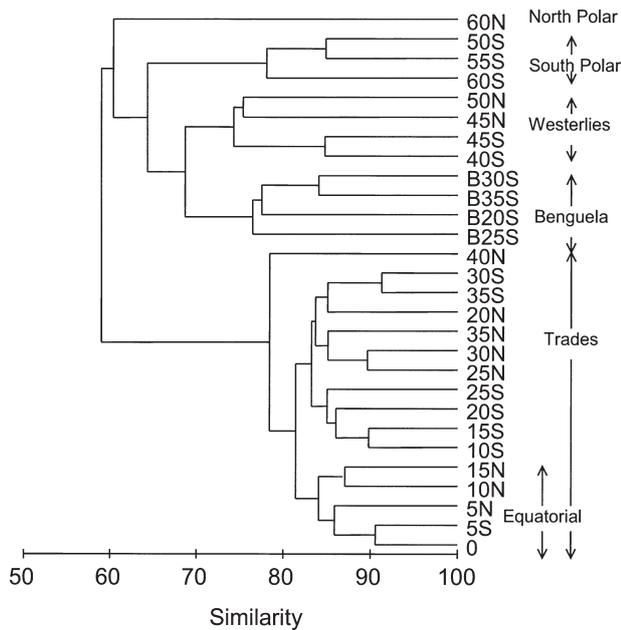


Fig. 5. Cluster analysis of epipelagic copepod assemblages from the Atlantic Ocean. Prior to analysis samples were pooled into bins of 5° latitude; mean values were double root transformed to reduce the effect of abundance structure, and a Bray-Curtis similarity matrix calculated. Stations from the Benguela were treated separately and are denoted by B. The identity of each latitudinal bin sample is shown. The samples map tightly onto the biome structure proposed by Longhurst (1998), as indicated by the area classification

Benguela, Trades, Westerlies and North and South Polar groups were all significantly different from each other ($p < 0.001$; Table 4). The equatorial sub-region was also significantly different from the rest of the Trades grouping at the 5% level ($p = 0.028$). Analysis at higher taxonomic levels (families and subfamilies) gave similar results, although the Benguela coastal biome was more similar to the Westerlies biome ($R = 0.209$ and $R = 0.136$ for subfamily and family respectively) than was the case for analysis of genera.

Longhurst's analysis also proposed a finer division of the 4 Atlantic biomes into 20 provinces (Longhurst 1998). We were only able to test this for the Trades and (South) Polar biomes, as within the other biomes numbers of stations and coverage were insufficient (Table 2). Within both biomes sample similarity was high overall, but cluster analysis and MDS indicated no clear spatial coherence be-

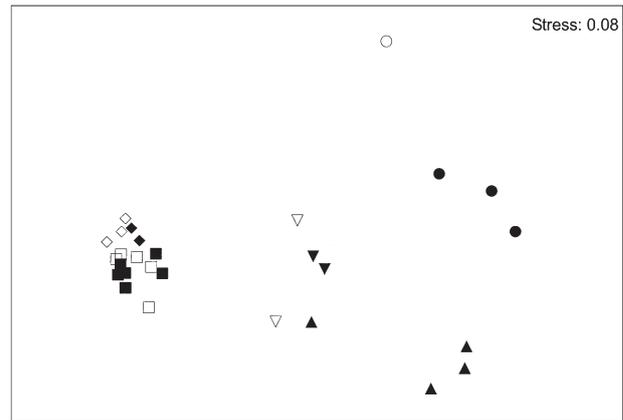


Fig. 6. Multi-dimensional scaling (MDS) plot of epipelagic copepod assemblages from the Atlantic Ocean. Prior to analysis, samples were pooled into bins of 5° latitude; mean values were double root transformed, and a Bray-Curtis similarity matrix calculated. Note the tight clustering of the data from the Equatorial and Trades regions, with the more dispersed Benguela and Polar samples. Data shown are grouped into Trades (■, □), Equatorial (◇, ◇), Westerlies (▼, ▼), Benguela (▲, △) and Polar (●, ○); filled symbols represent southern hemisphere and unfilled symbols northern hemisphere

tween samples to support further division into areas that would map onto Longhurst's provinces. Many factors might be responsible for this result, but it may simply imply that any further subdivision within these biomes must be based on the distribution of species rather than higher taxonomic levels such as genera.

Table 4. ANOSIM analyses of similarity between Atlantic surface copepod assemblages classified into the biomes proposed by Longhurst (1998). R: strength of the difference between groups; p: probability of R being attained by chance. No allowance for multiple tests has been made for the probabilities. The global result is the overall differences between groups (similar to 1-way ANOVA). SP: South Polar, W: Westerlies, T: Trades, B: Benguela, NP: North Polar

Groups	Genus		Sub-family		Family	
	R statistic	p	R statistic	p	R statistic	p
Global	0.892	<0.001	0.858	<0.001	0.748	<0.001
SP, W	0.784	<0.001	0.678	<0.001	0.494	<0.001
SP, T	0.977	<0.001	0.948	<0.001	0.839	<0.001
SP, B	0.652	<0.001	0.691	<0.001	0.609	<0.001
SP, NP	0.865	<0.001	0.689	<0.001	0.701	<0.001
W, T	0.814	<0.001	0.812	<0.001	0.575	<0.001
W, B	0.392	<0.001	0.209	0.003	0.136	0.010
W, NP	0.533	<0.001	0.693	<0.001	0.644	<0.001
T, B	0.915	<0.001	0.895	<0.001	0.704	<0.001
T, NP	0.970	<0.001	0.974	<0.001	0.975	<0.001
B, NP	0.699	<0.001	0.930	<0.001	0.818	<0.001
T, E	0.116	0.028	0.077	0.099	0.188	0.001

Community structure

The highest overall copepod abundances were found in the Polar biomes, although the variance was also very high, with total abundance ranging from 47 to $>4000\text{ m}^{-3}$. The Benguela and Westerlies regions also had relatively high copepod abundances with a mean of 754 and 630 m^{-3} respectively. Trades had low abundances with a mean of 227 m^{-3} and a minimum of 29 m^{-3} .

The South Polar biome was typified by a dominance of *Oithona*, small calanoids, *Calanus*, *Metridia*, and *Rhincalanus* with a few *Oncaea* and *Calanoides* (Table 2). Other genera were very rare, on average making up $<5\%$ of the total. The North Polar biome was also dominated by few genera: *Oithona*, with some *Calanus* and small calanoids. Other genera on average accounted for $<2\%$ of the total copepod abundance. Care is, however, needed in interpreting this region as samples were taken at 1 place over a 2 wk period. Previous studies at 59°N , 19°W , taken with $280\text{ }\mu\text{m}$ mesh to 500 m over the summer, have shown that the dominant copepod genera were *Oithona*, *Acartia*, *Calanus*, *Metridia*, *Oncaea*, *Euchaeta* and *Pleuromamma*. These made up $>85\%$ of the numerical abundance (Williams 1974, Williams & Hopkins 1975). The dominant Polar genera present appear to be generalists such as *Oithona* (Atkinson 1998) with the ability to change diet with season and food availability, or taxa such as the Megacalanidae and Eucalanidae, which overcome the spatially and temporally variable food supply by utilising large seasonal lipid stores (Conover 1988, Atkinson 1998).

The Trades biome included many more genera, with small calanoids, *Oithona*, *Oncaea*, *Metridia*, *Calanus*, *Corycaeus*, *Calanoides* and *Acartia* making up $\sim 90\%$ of the copepods. The Equatorial sub-region had a similar distribution of genera to the rest of the Trades biome, and subtle changes in the relative abundance of genera appeared to be responsible for its differentiation. The genera found within the Trades represent a wide range in life strategies, and the proportion of carnivorous copepods was also high.

The community composition of the mid-latitude Westerlies biome was generally intermediate between the Trade and Polar domains with common genera (small calanoids, *Oithona*, *Acartia*, *Oncaea* and *Pleuromamma*) making up $\sim 95\%$ of the copepods. Similarly, the overall abundance was intermediate. *Acartia* was more abundant, partly because of large numbers found at 1 station bordering on neritic waters.

The Benguela stations were most similar to the Westerlies, and had similar abundances, being dominated by few genera, including small calanoids, *Oithona*, *Metridia*, *Calanoides*, *Centropages* and *Oncaea*. Other

genera made up on average 1.5% of the numerical abundance. Overall the fewest genera were found in this region. Similar dominant copepods including *Calanoides*, *Centropages*, *Metridia* and various small calanoids were found by De Decker (1973). *Calanoides*, most abundant in this region, is known to be an upwelling specialist (Verheye et al. 1992). It stores lipids, and undergoes diapause and ontogenetic migrations allowing populations to maintain themselves within the system during periods of low productivity (Verheye et al. 1991). Species of *Centropages* are frequently coastal taxa, and *Centropages brachiatus* has been found to be prevalent in the more seasonal southern Benguela region (Verheye et al. 1992). *Centropages* are also omnivorous (Turner 1987) and have been found to have resting eggs (Mauchline 1998 and references therein). Such adaptations allow it to exploit a seasonal food supply within a shelf ecosystem and survive periods of low productivity. The resting eggs may tend to sink and thereby prevent it from colonising similar deep-water, open-ocean locations.

DISCUSSION

Three key aspects of these results are the large-scale patterns in diversity, the variations in the assemblage structure, and the nature of the underlying mechanisms governing these.

Large-scale patterns in diversity

Strong and symmetrical latitudinal gradients in diversity were apparent within our data at all taxonomic levels investigated (Figs. 2 & 3). The nature of the latitude-taxon richness relationship was somewhat different to those reported for copepods and other groups by Boltovskoy et al. (1999), who showed a slight reduction in species diversity around the equator relative to that seen at the transition region around 35 to 40°S , where cold and warm water faunas mix. This feature was not apparent in our South Atlantic data, and although in the North Atlantic the number of genera did increase slightly at 35°N , the number of samples obtained in this region was also greater. However, the richness per sample was not higher than expected (Fig. 2A).

Detailed regional studies carried out in the Atlantic (Roe 1972, 1984) and in the Southern Ocean (Hopkins 1985, Hopkins & Torres 1988) are in broad agreement with our study in terms of the numbers of copepod genera found in near-surface waters. At 28°N using $330\text{ }\mu\text{m}$ mesh to sample the upper 100 m, Roe (1972) found a total of 38 calanoid genera, which when

grouped according to our protocols (see 'Materials and methods') is equivalent to 25 genera and compares to 29 genera found around 30°N in this study. Following a similar treatment of data obtained by Roe (1984) at 44°N, 18 genera (total 23) compares to 22 found in this study. In the Southern Ocean at ~65°S, 17 (total 25) and 14 (total 19) genera (Hopkins 1985, Hopkins & Torres 1988 respectively) compare to our 60°S mean of 15 copepod genera. Thus more detailed studies show similar latitudinal trends although absolute numbers of genera found were greater.

Samples from the Benguela region showed low generic richness relative to oceanic stations at comparable latitudes. The Benguela is however an upwelling region and such areas typically have a less diverse fauna (Angel 1997).

When data from the Benguela upwelling region are excluded, the latitudinal variation in sample taxonomic richness at generic, family and superfamily levels was smooth. At all taxonomic levels the relationship of richness with latitude was well described by a quadratic regression (Table 3). However, other aspects of diversity suggested that changes in community structure were more abrupt, with a sharp change occurring at ~40°N/S coincident with a sea surface temperature of ~17 to 20°C (Figs. 3 & 4A). At low latitudes and high sea surface temperatures copepod communities were characterised by high stable taxonomic diversity (Δ) and a relatively even distribution of genera within samples. In contrast, at high latitude and low sea surface temperature communities showed large variation in overall diversity, evenness and distinctness. Samples from the Benguela system fitted into this second category indicating that copepod assemblage structure in upwelling regions was more closely correlated with the thermal or other characteristics of the habitat than with latitude.

Assemblage structure of surface copepods

Community structure derived from the pooling of samples within 5° latitudinal bands showed a similar pattern to univariate diversity analyses, but also provided extra information on biogeographic patterns. The groupings resulting from the cluster and MDS analyses (Figs. 5 & 6) closely paralleled Longhurst's (1998) division of the ocean into major biomes. This distinction was apparent whether analyses were conducted at the level of genus, sub-family or family, indicating fundamental changes in community composition between these major divisions. Community structure in the oligotrophic Trades biome was uniform between 40°N to 35°S and it was here that all measures of diversity were highest. Star & Mullin (1981)

and McGowan & Walker (1979) have also demonstrated that Tropical Pacific zooplankton communities are very stable, with rank order of species remaining constant even when abundances changed. We also detected an equatorial grouping which was distinct from the rest of the Trades biome. This equatorial region, bounded to the North by the conjunction of the North Equatorial Current and North Equatorial Counter Current and to the south by the South Equatorial Current, is more productive than most of the trade wind domain due to the associated upwelling bringing nutrient-rich water into the euphotic zone and enhancing primary production. The copepod genera found here were broadly the same as in the rest of the Trades domain (Table 2), but abundances tended to be slightly higher, possibly reflecting the higher primary production levels.

In contrast, the production regime of the Westerlies biome becomes increasingly seasonal polewards, due to winter mixing, and primary and secondary production become increasingly uncoupled. Here diversity was found to be more variable, although MDS grouped the Westerlies stations north and south of the equator together, despite these being separated by some 80 degrees of latitude. The Polar biome, however, comprised north and south station groupings that were quite distinct from one another. Broadly similar niches may be present, but different genera appear to have evolved similar life-history strategies. However, the limited sampling of the North Polar biome restricts its comparability with the South Polar biome (see 'Materials and methods' and 'Results').

Our study has identified changes in community structure at the taxonomic level of genus and above, which are coincident with some of the more pronounced biogeographic boundaries that have been identified by the more classical approach based on presence and absence of species. Whether analysis of our data to species level would have permitted a further subdivision of biomes into their component provinces as defined by Longhurst (1998) is an intriguing question. The nature of the faunal barriers, which might limit plankton dispersal in the oceans, is still not entirely clear. Many of the horizontal gradients at watermass boundaries are weak relative to vertical gradients, and are too weak to limit species distributions which tend to form a continuum, being characterised by core regions and regions of expatriation (Angel 1997). We might, therefore, ask how closely we would expect zooplankton distributions to map onto provinces determined from 1 set of discontinuities for primary producers. Although data are limited, evidence suggests that Longhurst's provincial definition is robust at least in the North Atlantic for picophytoplankton across 7 provinces (Li & Harrison 2001), and

Harrison et al. (2001) also found regional distinctions in acoustic backscatter, which is a first-order index of macrozooplankton/micronekton biomass.

Thus the regional definitions of Longhurst (1998), which have been shown to be robust for the primary producers, also appear to influence the diversity and abundance of higher trophic levels, suggesting a strong element of bottom-up control. However, copepods and many other planktons often have flexible feeding strategies (Mauchline 1998 and references therein) and in many cases are long-lived in relation to the temporal and spatial scales of physical forcing that underlie the differences in production characteristics that define Longhurst's provinces. One clear pattern to have emerged from studies of copepod life-histories is the importance of the degree of seasonality in their food supply. Since seasonality varies with latitude, and hence covaries to some extent with mean surface temperature, it is possible that seasonality plays a role in governing community diversity (see next section).

As our study concentrated only on the upper 200 m of the ocean and used 200 μm mesh nets, it will have underestimated the absolute diversity of the entire water column. Within a number of copepod groups, shifts in depth distribution with respect to latitude have been observed. A clear example is the Euchaetidae, members of which all generally have meso-bathypelagic distributions polewards of 40°S compared to their more epi-pelagically distributed tropical dwelling congeners (Bradford et al. 1983, Ward & Shreeve 2001). The extent to which these differing distributions may also be largely the result of changes in patterns of production and community function are examined below.

What controls copepod diversity?

Establishing precisely what factors regulate zooplankton diversity has proved a difficult task. Numerous ideas have been advanced to explain observed patterns although a coherent body of theory has yet to emerge. Studies in the North Pacific gyre by McGowan & Walker (1979, 1985) have provided the basis for assessing the importance of resource partitioning and disturbance perturbation as possible regulators over a variety of different temporal and spatial scales, although in neither case was supportive evidence found. A number of environmental factors have also been proposed as regulators of zooplankton diversity and in particular as producing the latitudinal diversity gradients seen within a wide number of taxa (see Rohde 1992, Rutherford et al. 1999, Gaston 2000).

Although null models based on simple geometry can predict latitudinal clines in diversity (Colwell & Hurltt 1994), latitude is not itself generally regarded as a

major driver of large-scale patterns in diversity (Gaston 2000). What has attracted considerable attention, however, has been a number of correlates of latitude, such as primary productivity, energy availability and the surface area of provinces.

For example, a recent study of foraminifera showed diversity to be positively correlated with that of sea surface temperature (Rutherford et al. 1999). The proposed mechanism was that the thermal structure of the near-surface ocean provided a greater number of niches in the tropics and subtropics compared to polar waters. Such a suggestion is in our view inconsistent with the deep seasonal mixing of the oceans that occurs polewards of ~40° latitude and does not satisfactorily explain the step-change in community structure observed in our study at the boundary between the tropical and subtropical watermasses. With few exceptions those factors that most influence physical structure and circulation within the oceans are highly variable in space and time and do not decline in a simple manner from the tropics to the poles. Given the congruence of our groupings of 5° mean data with major biomes that are characterised by different temporal patterns of production, we suggest that copepod diversity also reflects this and in particular the changes in seasonality that occur in moving from the tropics to the poles. In the tropics and subtropics, production cycles are of generally low amplitude, continue through the year, and primary and secondary production are closely coupled. This leads to a retentive system in which diversity is characteristically high (Conover 1979, Longhurst & Pauly 1987). In cold temperate and Polar regions, production and consumption become increasingly uncoupled and here diversity is lower and variance higher (Fig. 3).

A traditional view has been that in a fluctuating environment the ability of an organism to exist in as wide a range of habitats as possible, and to have a wide trophic scope, is adaptive, whereas greater environmental stability allows more specialisation (Valentine 1973). Thus niche width might be expected to be greater at higher latitudes, with a corresponding increase in the number of generalist taxa (Angel 1993). Fig. 7 shows the proportion of carnivorous as compared to herbivorous and omnivorous copepods with respect to latitude. Although a simple analysis, this does clearly show the increased proportion of carnivorous copepod taxa in the tropical and subtropical epipelagic and the corresponding increase in the proportion of herbivorous or omnivorous particulate feeders to the north and south. This parallels the changes in mesozooplankton composition between biomes, in which carnivorous groups were more abundant in the Trades and the proportion of copepods lower than in the other biomes (Longhurst & Pauly 1987, Longhurst

1998). We therefore conclude that copepod diversity is influenced primarily by large-scale variation in the seasonal patterns of primary production, and by the degree of coupling between primary and secondary producers. Since these patterns vary with latitude, a correlation with temperature emerges simply as an association, and temperature per se cannot be a major driver of diversity.

Along the latitudinal gradient, there is evidently a fallout in genera rather than a replacement. Those genera that dominate the high latitudes also tend to be present at low latitudes (although the species may be different). By examining which genera are abundant at high latitudes, we may find more direct evidence as to the underlying mechanisms determining community structure. There is a substantial body of work on polar copepod communities, from which it appears that 2 principal life history strategies allow genera to be successful: generalists, and lipid storers with diapause stages (Atkinson 1998). *Oithona*, being omnivorous/detritivorous, typifies the generalist with a wide range of feeding mechanisms, enabling an extended feeding period. The lipid storing strategy is typified by genera such as *Calanoides* and *Calanus*, which are herbivorous in summer, have a short reproductive period and overwinter in diapause at depth. Thus it appears that it is the seasonality and patchiness in food supply, overcome by either storing or by switching diet, that make it hard for other groups to survive in Polar environments. Similarly, in the Benguela upwelling, the abundant genera are either omnivorous or lipid storing (Verheyen et al. 1992) and production is seasonal at least in the southern Benguela, and patchy throughout the upwelling system. In the Trades, production is continuous, and the environment generally more stable. Greater specialisation such as carnivory is evident in the copepods (Fig. 7). A variety of mechanisms have been proposed which will tend to further increase the diversity of already species-rich assemblages, even more so through biological interactions (e.g. predation: Paine 1966, Janzen 1970; competition: Dobzhansky 1950, Huston 1979; biotic spatial heterogeneity: Huston 1979, Thiollay 1990). There is also growing evidence that greater diversity will serve to stabilise ecosystem processes further (Berlow 1999, McCann 2000) through the action of weak interactive forces.

A final comment: benthos and history

A recent detailed study of geographical patterns in the species richness of continental-shelf benthic marine gastropods has also revealed steep gradients (Roy et al. 1998). In the western Atlantic, species richness pooled by bins of 1° latitude drops from ~900 to

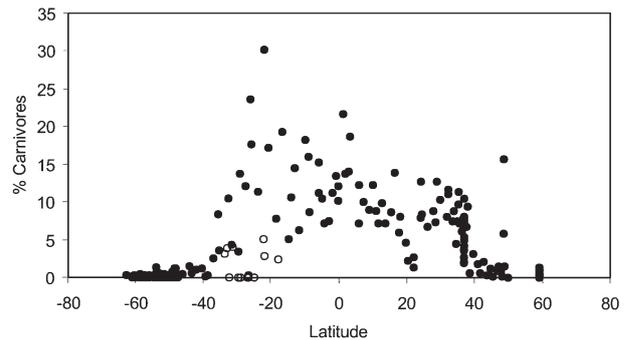


Fig. 7. Relationship between latitude and the proportion of carnivorous individuals in surface copepod assemblages from the Atlantic. Data for each sample are plotted individually (●); data for the Benguela upwelling region are plotted separately (○), and excluded from statistical analyses. By convention latitudes S are shown negative

~100 species bin^{-1} between 25 and 35°N. Although this step change in benthic gastropod diversity occurred at slightly lower latitude than in our copepod data, it is coincident with a change in SST of 17.5 to 22°C, and this sharp change in diversity was attributed to trophodynamic processes. Rex et al. (2000) also found latitudinal gradients in species richness of the deep-sea benthos of the North Atlantic. These environments are not subject to the climatic fluctuations found in the overlying surface waters, but they are affected by the near-surface productivity regimes, through the variation in rates of vertical flux of organic material. Thus seasonality in primary production is implicated in the reduction of benthic diversity at higher latitudes. Although benthic latitudinal gradients are consistent with the proposed effects of seasonality, it remains to be seen whether changes in community structure are consistent with Longhurst's framework.

We therefore conclude that the global patterns we have observed in the diversity and community structure of pelagic copepods are related to the temporal patterns of primary and secondary production, which are critical in defining the biomes and provinces proposed by Longhurst (1998). This primary control by seasonality is essentially an equilibrium, an ecological explanation for pelagic copepod diversity. It contrasts with the benthos, where it has been argued that large-scale biogeographic patterns of diversity have a strong historical legacy (Crame & Clarke 1997). Whilst the differences in dispersal ability and environmental structure differ markedly between the pelagic and benthic marine realms, it remains an open and intriguing question as to whether 1 single process explanation, or a suite of processes, will prove to be the dominant driver determining diversity in all habitats, terrestrial and marine, pelagic and benthic.

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