Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of the Paratethys

MARTIN ZUSCHIN, MATHIAS HARZHAUSER AND KARIN SAUERMOSER

LETHAIA

Zuschin, M., Harzhauser, M. & Sauermoser, K. 2006 03 31: Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of the Paratethys. *Lethaia*, Vol. 39, pp. 65–78. Oslo. ISSN 0024-1164.

The best hope for understanding global diversity patterns is to compare local assemblages, which are mostly preserved in taphonomically-complex shell beds. The present study investigates the variability in faunal composition and diversity at the scale of a single outcrop. A total of 152 species (3315 shells) occurred in 25 samples from 5 tempestitic shell beds. Although sampling intensity was high, total species richness was not captured by far at the hierarchical levels present (outcrop, shell beds, samples) because the majority of species is rare. In contrast, sampling intensity was sufficient to cover the most abundant species, as indicated by stable evenness values. Four taxa dominate the assemblage, but their rank order differs strongly between individual shell beds and individual samples; significant differences between some shell beds are evident for faunal composition, and one shell bed differs from all others with respect to species accumulation curves. Within shell beds, rarefaction curves are generally characterized by strongly overlapping confidence intervals, but outliers occur in three of five shell beds. Patchiness is additionally indicated by a wide scatter of diversity indices in some shell beds and by a wide scatter of samples of one shell bed in an ordination on faunal composition. Most of the outcrop-scale variability in faunal composition and diversity can be related to differences between shell beds. This suggests that sampling a single shell bed of the outcrop is insufficient to characterize the local fauna and its diversity, even when sampling intensity (i.e. the number of samples and shells) within the shell bed was high. Similarly, a single sample from such a shell bed may not be sufficient to characterize its diversity, even when the number of counted shells was high. It is therefore confirmed that sampling strategy and sampling intensity are crucial to confidently characterize the shelly assemblages at such a small spatial scale and that dispersed sampling effort with many small replicate samples will characterize a local assemblage and its diversity better than a few large samples. Diversity comparisons of individual samples between localities must account for the high variability present at the smaller spatial scale, as observed in our study. □ *Evenness, local diversity, shell beds, spatial variability, tempestites.*

Martin Zuschin [martin.zuschin@univie.ac.at], Institut für Paläontologie, Universität Wien, Althanstrasse 14, A-1090 Vienna, Austria; Mathias Harzhauser [mathias.harzhauser@nhm-wien.ac.at], Naturhistorisches Museum Wien, Burgring 7, A-1014 Vienna, Austria; Karin Sauermoser, Institut für Paläontologie, Universität Wien, Althanstrasse 14, A-1090 Vienna, Austria; *21st January 2005, revised 22nd November 2005.*

Phanerozoic diversity trends can be studied at different scales of observation, ranging from local to global (e.g. Sepkoski 1988), and patterns retrieved from one level of analysis may not be similar to those from another (e.g. Johnson 2003; Adrain & Westrop 2003; Willis & Whittaker 2002). Changes in global richness might result from increasing local richness as local communities become more complex (Valentine 1969; Bambach 1977), from variations among major regions (Valentine *et al*. 1978; Miller 1997a; Jablonski 1998) or could be decoupled from local or regional diversity (e.g. Adrain & Westrop 2000). In the latter case, local and regional signals can be buried in analyses that begin on the global scale (Vermeij & Leighton 2003), and the best hope for understanding global diversity patterns is to collect information on local assemblages (Johnson 2003). For this reason, studies that trace diversities at such fine levels of resolution are of great interest and should be based on standardized ecological sampling (Jackson & Johnson 2001).

The present study deals with two important aspects of diversity patterns of local assemblages. First, the information on local assemblages is mostly preserved in stratigraphically-complex shell beds (Kidwell 1991; Kidwell & Brenchley 1994) whose palaeoecological features (e.g. diversity and trophic structure) may not

Taylor & Francis
Taylor & Francis Group

DOI 10.1080/00241160600578687

be directly comparable because of differing taphonomic histories (Norris 1986; Kidwell 1991; Zuschin *et al*. 2005). Among shell beds, tempestitic and turbiditic deposits are ubiquitous throughout the Phanerozoic (Kidwell & Brenchley 1994; Li & Droser 1997) and such event beds are the source for most palaeontological studies of benthic faunas (cf. Kowalewski & Bambach 2003, p. 5). Second, local assemblages are typically characterized by patchy distributions in faunal compositions; sampling strategy and sampling intensity are therefore crucial to confidently characterize shelly assemblages at such a small spatial scale (Lafferty *et al*. 1994; Bennington 2003; Webber 2005). In general, a dispersed sampling effort with many small replicate samples will characterize a local assemblage better than a few large samples (Bennington 2003). The problem of patchiness, however, should be smaller in event beds because transportation should homogenize originally patchy population distributions and make relative abundance more uniform (Olszewski & West 1997; Bennington 2003), although even in storm beds some of the original, (par)autochthonous patchiness can be preserved (Miller 1997).

The present study deals with faunal and diversity differences between and within tempestitic shell beds at a single outcrop in the middle Miocene of the Central Paratethys. It is part of a larger project that deals with Miocene molluscan associations in Austria and adjacent countries, which almost exclusively occur in shell beds. A few assemblages in the shell beds here experienced only minor transport or habitat mixing (e.g. Harzhauser & Kowalke 2002; Zuschin *et al*. 2004a), but many of them are distinctly allochthonous tempestitic deposits, with transport distances ranging from hundreds of meters to several kilometers (e.g. Mandic *et al*. 2002; Zuschin *et al*. 2004b; this study and unpublished data). Any study on diversity patterns in the Middle Miocene of the Central Paratethys would therefore almost inevitably include allochthonous shell beds (e.g. Kowalewski *et al*. 2002). The aim of our study is to investigate the heterogeneity of faunal composition and diversity at the scale of a single outcrop. Specifically, we want to answer the question whether there are significant differences in diversity between and within shell beds. Significant differences between shell beds would indicate that sampling a single shell bed is not sufficient to characterize the locality's diversity. Any significant diversity differences within shell beds would point to small-scale patchiness within allochthonous shell beds despite transport-related faunal homogenization and would also suggest that a single sample from such a shell bed does not characterize its diversity at the local scale.

Material and Methods

Geological setting

The studied samples derive from the middle Miocene Grund Formation in the Austrian part of the Molasse Basin (Fig. 1) (Coric *et al*. 2004). Palaeogeographically, this basin was part of the Central Paratethys Sea – a northern satellite sea of the Western Tethys (= Proto-Mediterranean) that was formed in the early Oligocene by the rising Alpine island chain, which acted as a geographic barrier (Rögl 1998). Due to the strong tectonic control, the subsequent evolution of the Paratethys differed considerably from that of the adjacent Mediterranean and is reflected in the regional stratigraphic stage system for the Paratethyan sedimentary succession (Rögl 1998; Steininger & Wessely 2000; Harzhauser *et al*. 2002).

According to this regional stage system, the Grund Formation is part of the lower Badenian stage, which is correlated with the Langhian of the Mediterranean standard scale. An early middle Miocene age based on the occurrence of the planktonic foraminifera *Praeorbulina glomerosa circularis* was demonstrated by Rögl *et al*. (2002), who correlated the deposits with plankton zone M5b and nannoplankton zone NN5. The characteristic benthic foraminiferal assemblage allows correlation with the lower Lagenidae Zone of the Vienna Basin ecostratigraphic zonation (*sensu* Grill 1941, 1943).

Six sections were studied at the Immendorf locality, but deposits with undisturbed lateral and vertical extension were only found in sections C and D (Figs. 1 and 2). Due to post-depositional slumping of the deposits, most likely during the Pleistocene ice ages, only a rough correlation between sections was possible; section D contains the younger deposits. The studied sections are characterized by a dominance of autochthonous pelitic sediments and interbedded allochthonous psammitic event beds. These event beds are several-decimeter-thick polytaxic skeletal concentrations (*sensu* Kidwell *et al*. 1986) with sharp erosional bases, graded bedding, and a densely packed (bioclast-supported) biofabric. Sharp erosional bases and graded bedding identify the shell-rich psammitic layers as the product of high-energy, short-term events, which are interpreted as proximal tempestites (Fürsich & Oschmann 1993). They are very similar to the shell beds found at a slightly older locality in the Grund formation (Roetzel & Pervesler 2004; Zuschin *et al*. 2004b, 2005) and are also interpreted as allochthonous deposits. The faunal composition of the shell beds, their high diversity and ubiquitous abrasion features of the shells point to a wave- or current-agitated, mixed soft- and hard bottom shelf environment as the source area for the tempestites. The shell beds have a sandy matrix and are preserved in

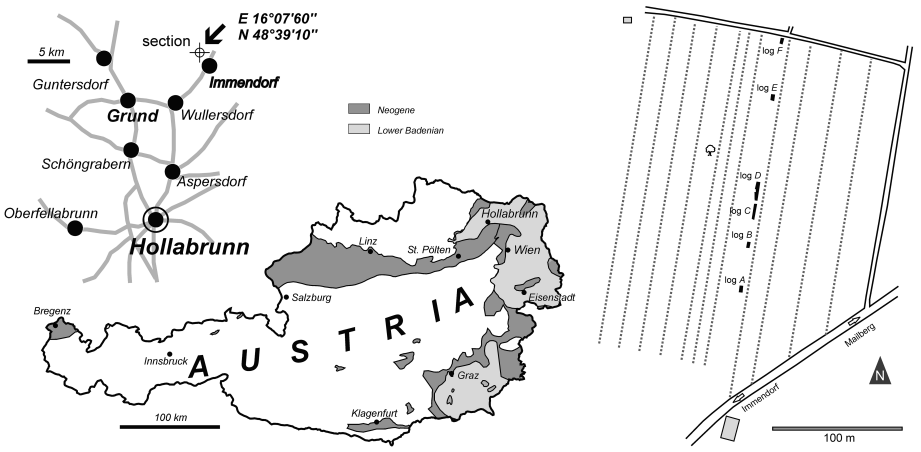

Fig. 1. Study area and studied artificial trenches (log A–F) in the farmland N of the village Immendorf, lower Austria.

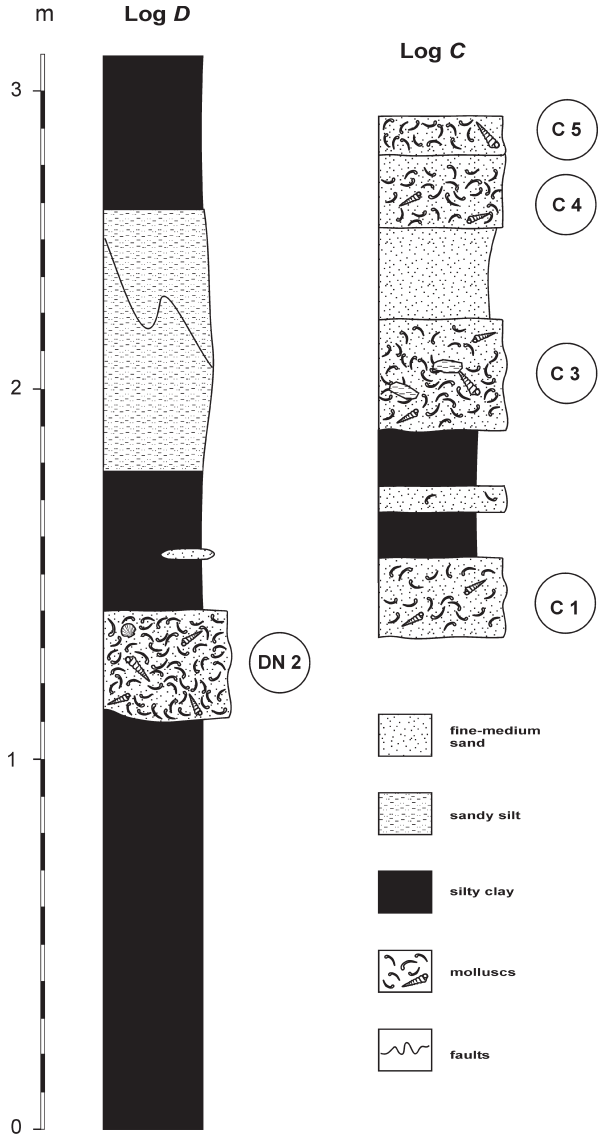

Fig. 2. The two studied logs with shell beds (modified after Sauermoser 2004).

deeper-water mudstones (Fred Rögl personal communication, November 2005), which contain no macrofossils. Finally, the distance to the paleo-coastline was at least several kilometers.

Sampling

No natural outcrops or roadcuts are available in the area of the Grund Formation. Therefore, six deep trenches were excavated with power shovels in the farmland north of the village Immendorf, north of Hollabrunn in northern Lower Austria (Fig. 1). Two artificial outcrops of lower Badenian deposits, which contained 5 shell beds, were examined (Fig. 2) and 25 quantitative bulk samples (5 samples per shell bed) were taken. The total sample weight studied is 28.937 kg; the mean weight per shell bed is 5.785 ($\pm$0.824) kg, with a range from 4.635–6.938 kg. The 5 samples per shell bed were taken in a lateral distance of 30 cm from each other. The mean weight per sample is 1.157 kg ($\pm$0.514) with a range from 0.594–2.484 kg (Table 1). The sediment was wet sieved through a 1 mm screen and the material $>$1 mm was quantitatively picked for all biogenic components, which included mainly molluscs but also crustaceans and serpulids, under a binocular microscope. Among these higher taxa, only the molluscs were used for this study. Each disarticulated valve of bivalves was treated as an individual; 3315 shells were counted and sorted into 152 species (51 bivalves, 98 gastropods, 3 scaphopods) (see Online data set).

Analysis of faunal composition

The data set (25 samples, 3315 shells, 152 species) was used to study differences between shell beds and small-scale variability within shell beds at different numerical scales, i.e. absolute *versus* relative numbers, and raw *versus* transformed abundances. The choice of percentage data and transformation is based on

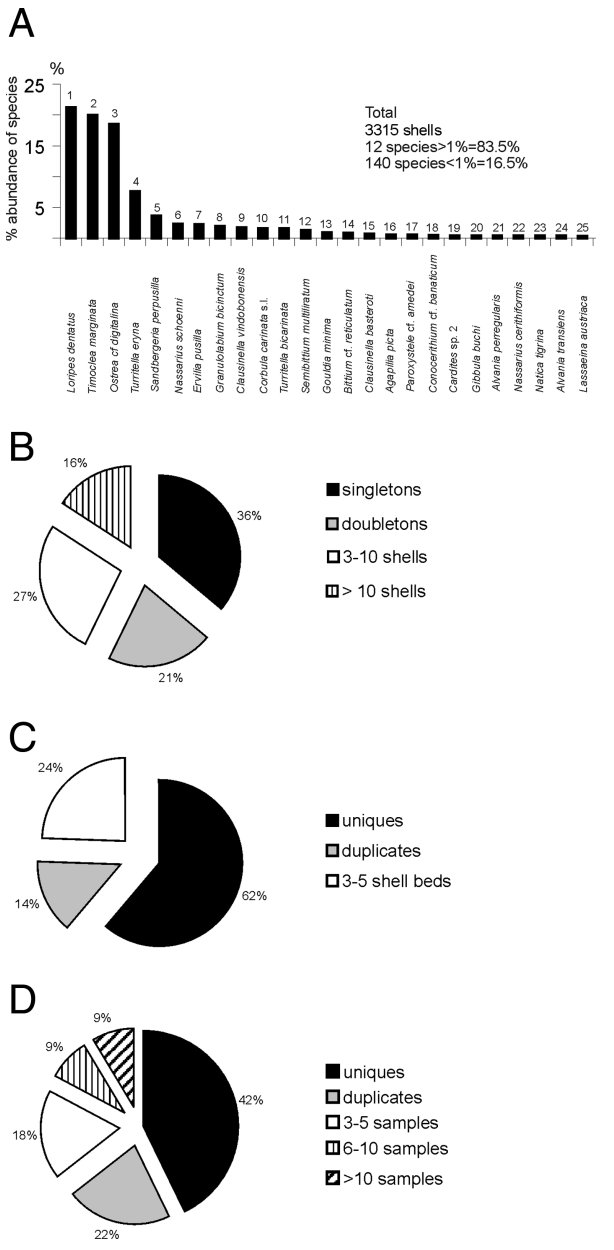

Fig. 3. Taxonomic composition, percentage abundance and occurrence of the molluscan assemblage at Immendorf. □A. Percentage abundance of quantitatively important species in the total assemblage. □B. The percentage of species in the total assemblage in four abundance categories. □C. The percentage of species of the total assemblage in shell beds in three occurrence categories. □D. The percentage of species of the total assemblage in samples in five occurrence categories.

palaeontological and statistical considerations. Use of relative numbers should usually be avoided because valuable ecological information is contained in the abundance data (Clarke & Warwick 1994). Relative numbers, however, can be useful if differing volumes of sediment are sampled, in which case absolute numbers of individuals are not comparable between samples (Clarke & Warwick 1994). Which aspects of the community we wish to study determines the choice of transformation and this choice can affect the conclusion of any study. Therefore, the choice of transformation is more a biological than a statistical question (Clarke & Warwick 1994). The similarities of untransformed data will unduly be dominated by the counts of the most abundant species. The larger abundances in the original data matrix will often be extremely variable in replicate samples and a transformation of the original values will down-weight the importance of the very abundant species so that the less dominant species play some role in determining similarities of two samples (Clarke & Warwick 1994). For the present study, we chose to compare the results from data sets with absolute abundances with those of relative abundances, each using untransformed data (emphasizing the most abundant species), square-root transformed data (which emphasize the influence of species with intermediate abundances), fourth-root transformed data

Table 1. Basic data for the studied samples and shell beds.

	Weight (in kg)	Number of individuals	Number of species	Shannon-Wiener index	Simpson index
Samples					
DN2-1	0.92	141	30	2.42	6.31
DN2-2	1.31	214	46	2.91	12.16
DN2-3	0.75	173	38	2.86	11.16
DN2-4	1.07	290	64	3.20	13.51
DN2-5	1.72	432	62	2.70	6.49
C1-1	0.59	30	7	1.65	4.44
C1-2	0.65	56	13	1.89	4.57
C1-3	0.65	43	13	2.24	9.12
C1-4	1.24	160	18	2.16	6.26
C1-5	2.48	64	15	2.17	7.12
C3-1	0.62	47	11	1.98	6.04
C3-2	0.80	56	10	1.66	4.23
C3-3	0.82	97	16	1.94	5.19
C3-4	0.77	95	18	2.06	5.44
C3-5	1.62	193	28	2.26	6.05
C4-1	0.62	26	8	1.78	5.60
C4-2	1.10	104	14	1.82	4.59
C4-3	0.91	97	20	2.14	5.68
C4-4	1.38	144	21	2.07	4.94
C4-5	1.96	193	27	2.19	5.93
C5-1	1.35	96	12	1.75	4.77
C5-2	1.22	89	14	1.93	4.90
C5-3	1.06	146	21	1.96	4.56
C5-4	1.07	99	14	1.81	4.13
C5-5	2.24	230	29	2.05	4.48
all samples	28.93	3315	152	2.81	7.76
Shell beds					
DN2	5.78	1250	128	3.16	9.65
C1	5.61	353	30	2.27	6.23
C3	4.64	488	43	2.23	5.6
C4	5.97	564	39	2.23	5.54
C5	6.94	660	43	2.09	4.74
all shell beds	28.93	3315	152	2.81	7.76

(emphasizing the influence of rare species) and presence/absence data (putting equal weight to all species present) (Field *et al*. 1982).

In order to test the significance of taxonomic differences between shell beds, analysis of similarity (ANOSIM, Clarke & Warwick 1994) based on the Bray-Curtis similarity coefficient (Bray & Curtis 1957) was applied. Of the numerous similarity coefficients that have been suggested over the years, the Bray-Curtis coefficient has become particularly common in ecological work (Clarke & Warwick 1994). The important message of the pairwise tests of the ANOSIM analysis is usually not so much the significance level (which can often be low because of few replicates in each group), but the pairwise R-values; the latter give an absolute measure of how separated the groups are, on a scale of 0 (indistinguishable) to 1 (all similarities within groups are less than any similarity between groups). With R values >0.75, groups are well separated; with R values >0.5, groups are overlapping but clearly different; with R values >0.25, groups strongly overlap; and with R values <0.25, groups are barely separable (Clarke & Gorley 2001). A similarity percentage analysis (SIMPER, Clarke & Warwick 1994) was performed to determine which species were responsible for the greatest similarity within shell beds, and which were most responsible for dissimilarity between shell beds. Within shell beds, those species for which the ratio of mean similarity to standard deviation of similarity is >1 typify the sample group. Between shell beds, good discrimination of a species is indicated by a high ratio of mean dissimilarity to the standard deviation of the dissimilarity (Clarke & Warwick 1994). Only species with a ratio of average dissimilarity/SD dissimilarity >1 are listed in the comparisons.

Non-metric multidimensional scaling (MDS, Kruskal 1964) was used as an ordination method to provide a visual comparison of the pattern of Bray-Curtis values among shell beds. In the ordination plot, points close to one another represent samples that are more similar in taxonomic composition than points farther away from another. MDS was used and run with 30 random starting configurations. The stress value in this analysis indicates how faithfully the high-dimensional relationships among the samples are represented in the 2-dimensional ordination plot. Potentially useful 2-d plots should have a stress value <0.2 and this value should be attained from several restarts of the analysis (Clarke & Warwick 1994). In this study, the minimum stress values were attained from 30 random starting configurations and the frequent recurrence of relatively low values (0.09–0.16 for comparisons between shell beds) indicates that the high-dimensional relationships among the samples are represented faithfully in the 2-d ordination plot (Clarke & Warwick 1994). The statistical analyses were performed using the software package PRIMER (Clarke & Warwick 1994).

Analysis of diversity patterns

Diversity was measured as species richness and as evenness, which is based on the proportional abundance of species (for a review see Magurran 2004). The Simpson index, which is affected by the 2–3 most abundant species, and the Shannon-Wiener index, which is more strongly affected by species in the middle of the rank sequence of species, were used as measures of evenness (see Gray 2000 for discussion). Both indices were calculated using the program EstimateS (Colwell 2000). The Simpson index was calculated as the inverse $(1/D)$ of the equation

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

where S = the total number of species, n_i = the number of individuals in the ith species and N = the total number of individuals. The Shannon-Wiener index was calculated with the equation

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where S = the total number of species, and p_i = the proportion of individuals found in the ith species. Species richness, the Simpson index and the Shannon-Wiener index were chosen because they are the most commonly employed measures of diversity (Lande 1996). It should be mentioned, however, that the underlying statistical distribution of a sample will generally influence the constancy of evenness measures and that the Shannon-Wiener index is particularly sensitive to sample size (Lande 1996; Magurran 2004; Buzas & Hayek 2005).

Diversity curves were used to compare species richness between and within shell beds. For shell beds, species accumulation curves were computed using the program EstimateS (Colwell 2000) for each shell bed, with 50 sample order randomizations without replacement. Samples are added to the analysis in random order and each sample is selected only once. By randomizing many times, the effect of sample order can be removed by averaging over randomizations, producing a smooth species accumulation curve (Colwell 2000). For samples within shell beds, rarefaction curves were computed using the program Past (Hammer *et al*. 2001, 2004).

Results

A total of 152 species from 3315 shells occurred in the 25 samples from five shell beds (Online data set). Four taxa (the bivalves *Loripes dentatus*, *Timoclea marginata*, *Ostrea* cf. *digitalina*, and the gastropod *Turritella eryna*) dominate the molluscan fauna of the Immendorf locality. In the total assemblage they make up 67.3% of the shells (Fig. 3A); their mean percentage abundance is 71.4% in the 5 shell beds, with a range from 50.8–81.9% in individual shell beds (Fig. 4), and a range from 42.1–89.6% in individual samples (Online data set). These four taxa are always among the most characteristic faunal elements of each shell bed. The only exception is shell bed DN2, where *Nassarius schoenni*, *Sandbergeria perpusilla* and *Ervilia perpusilla* are more quantitatively important or more characteristic than *Ostrea* cf. *digitalina* and *Turritella eryna* (Fig. 4; Table 2). The rank order of the four dominant taxa relative to each other, however, differs strongly between individual shell beds (Fig. 4) and individual samples (Online data set). In addition, at the level of samples, other overall rather unimportant species like *Granulolabium bicinctum*, *Conocerithium* cf. *banaticum*, *Alvania perregularis* and *Natica tigrina* can be quantitatively important (Online data set).

The majority of the 152 species is rare: only 12 species contribute more than 1% to the total fauna, and more than half of the species occur with only one or two shells (Fig. 3B). More than three quarters of the species are restricted to one or two shell beds (Fig. 3C), and almost two thirds of the species occur in only one or two samples (Fig. 3D). Also, within shell beds the number of singleton and doubleton taxa is consistently higher than 50%, and the number of uniques and duplicates among samples is always more than 60% (Fig. 4). Diversity was evaluated for the total fauna, for individual shell beds and for each sample (Table 1; Figs. 5 and 6). Although the number of counted shells is relatively high (Table 1), species accumulation curves show that species richness does not level off for the site and for the shell beds, and rarefaction curves show that species richness does not level off for individual samples (Figs. 5 and 6). In contrast to species richness, evenness is very stable within shell beds and for the site overall: the Shannon-Wiener index and the Simpson index do not increase with sample size (Fig. 5).

Differences in faunal composition between shell beds are very similar for absolute abundances and percentages and for all levels of data transformation (Table 3), indicating a very robust data matrix. Shell bed DN2 consistently differs significantly from all others. For percentage data and all levels of transformation, shell bed C1 also differs significantly from shell beds C3, C4 and C5, but differences between C3, C4 and C5 are not significant (Table 3B). These results are virtually identical for analysis on absolute abundances, except for the lack of significant differences between shell beds C1 and C3 when using transformed data (Table 3A). These results are also reflected in the MDS, where shell bed DN2 is strongly separated from all other shell beds, and shell bed C1 shows only minor overlaps with C3 and C5. In contrast, C3, C4 and C5 show strong mutual overlaps in the MDS (Fig. 7). Differences in the proportions of the quantitatively important species are mostly responsible for significant differences between shell beds (Table 2, Appendix 1).

Huge differences are evident between the number of species in individual shell beds (range from 30–128) and between the number of species in individual samples (range from 7–64) (Table 1). These differences partly reflect different sample sizes, but the slopes of the diversity curves indicate also differences between shell beds and between samples in species abundance patterns (Fig. 8). Shell bed DN2 differs significantly from the other shell beds as indicated by the lack of overlaps of confidence intervals of species accumulation curves. In contrast, all other shell beds are very similar as indicated by strong mutual overlaps of confidence intervals.

Rarefaction curves of samples within shell beds are generally characterized by strongly overlapping confidence intervals and, correspondingly, only few examples for significant differences between samples are evident. In shell bed DN2, sample DN2–4 has a comparatively steep slope, and in shell bed C4 and C5 the slopes of samples C4–2 and C5–1 are comparatively gentle (Fig. 6).

Comparison of rarefaction curves of all samples is similar to comparison of species accumulation curves of shell beds. The five samples with the steepest slopes are from shell bed DN2. The more gentle slopes are from samples in shell beds C1–C5, which are largely indistinguishable based on overlaps of confidence intervals (Fig. 8).

Discussion

Sampling intensity and diversity

In this study the number of counted individuals is relatively high but species-sampling curves show that species richness does not level off for the site, individual shell beds or individual samples (Table 1; Figs 5, 6 and 8), a feature that is typical for Recent molluscan assemblages (e.g. Bouchet *et al*. 2002; Zuschin & Oliver 2005) and for samples from Cenozoic shell beds (e.g. CoBabe & Allmon 1994; Zuschin *et al*. 2005). This reflects the rarity of most species, which typically occur with few

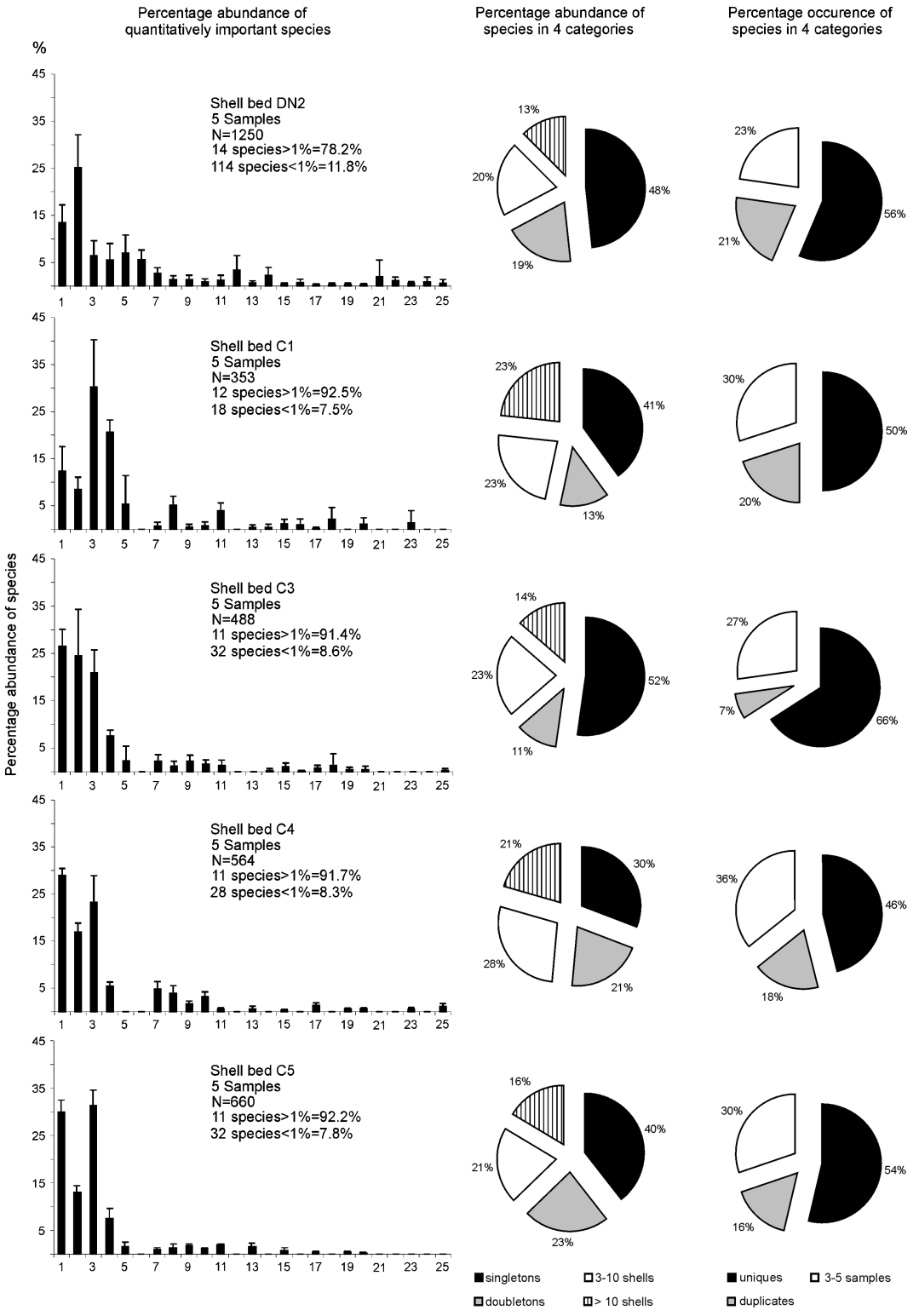

Fig. 4. Percentage abundance and occurrence of species among the five samples within each shell bed. The mean percentage abundances of the quantitatively important species are shown with the upper limit of the 95% confidence intervals. Numbering of species is according to numbers in Fig. 3A.

shells in few samples (Figs 3, 4). In contrast to species richness, however, the Simpson index, which is affected by the 2–3 most abundant species, and the Shannon-Wiener index, which is more strongly affected by species in the middle of the rank sequence of species (for discussion see Gray 2000), do not increase with

Table 2. Characteristic species for each shell bed, calculated for standardized data set and square-root transformed abundances using similarity percentage analysis (SIMPER, [Clarke & Warwick 1994]). Characteristic species are those for which the ratio of average similarity to standard deviation of similarity is >1.

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%
shell bed DN2				
Average similarity: 50.42				
Timoclea marginata	65.2	8.59	6.21	17.05
Loripes dentatus	33.2	6.3	6.87	12.5
Ostrea cf. *digitalina*	14.8	3.91	5.11	7.76
Nassarius schoenni	15.2	3.71	3.27	7.35
Sandbergeria perpusilla	17	3.43	2.07	6.81
Ervilia pusilla	6.8	2.58	5.39	5.11
Turritella eryna	13.4	2.41	1.09	4.78
Clausinella vindobonensis	4	1.57	4.13	3.12
Granulolabium bicinctum	3.6	1.28	1.12	2.54
Nassarius cerithiformis	2.8	1.12	1.14	2.22
Corbula carinata s.l.	2	0.95	1.01	1.89
Turritella bicarinata	4	0.94	1.12	1.86
Gouldia minima	2	0.86	1.14	1.71
Natica tigrina	1.4	0.73	1.12	1.44
Neverita josephinia	1	0.72	1.14	1.43
Clausinella basteroti	1	0.72	1.14	1.43
Nassarius cf. notterbecki	1.4	0.69	1.08	1.37
Nassarius sp. 7	1	0.65	1.09	1.29
Setia laevigata	0.8	0.6	1.13	1.2
shell bed C1				
Average similarity: 64.42				
Ostrea cf. *digitalina*	20.2	15.43	4.87	23.94
Turritella eryna	15.6	13.86	21.83	21.52
Loripes dentatus	8.6	9.38	13.49	14.56
Timoclea marginata	5.8	8.28	8.17	12.85
Granulolabium bicinctum	3.6	6.08	4.31	9.44
Turritella bicarinata	2.4	5.26	3.94	8.16
shell bed C3				
Average similarity: 63.99				
Loripes dentatus	25.4	15.43	9.37	24.11
Ostrea cf. *digitalina*	18.8	13.25	7.81	20.71
Timoclea marginata	25.2	12.87	4.01	20.12
Turritella eryna	7.2	8.15	6.52	12.73
Clausinella vindobonensis	2.2	3.65	4.71	5.7
Ervilia pusilla	2.4	2.67	1.14	4.18
Corbula carinata s.l.	1.8	2.22	1.13	3.47
shell bed C4				
Average similarity: 63.23				
Loripes dentatus	31.2	15.79	9.07	24.97
Timoclea marginata	18.2	11.32	5.84	17.9
Ostrea cf. *digitalina*	30.4	8.61	1.14	13.61
Turritella eryna	5.6	6.15	3.42	9.73
Ervilia pusilla	3.6	4.44	2.08	7.02
Granulolabium bicinctum	2.6	3.76	3	5.95
Corbula carinata s.l.	4.8	2.94	1.16	4.65
Clausinella vindobonensis	2.4	1.85	1.14	2.92
Paroxystele cf. *amedei*	1	1.7	1.13	2.7
Donacilla cornea	0.8	1.5	1.1	2.38
shell bed C5				
Average similarity: 66.04				
Ostrea cf. *digitalina*	38.4	16.03	5.95	24.27
Loripes dentatus	42.4	15.88	13.39	24.05
Timoclea marginata	18	10.21	9.61	15.47
Turritella eryna	8.4	6.57	3.41	9.95
Turritella bicarinata	2.4	4.12	5.74	6.24
Clausinella vindobonensis	2.6	3.57	6.29	5.41
Corbula carinata s.l.	1.2	2.57	3.88	3.89

Table 2 (*Continued*)

increasing sample size either for individual shell beds or the site (Fig. 5). This indicates that incorporating more samples per shell bed would simply add more rare species, but would not change the rank order of the most abundant and the middle-ranked species. Therefore, the sampling intensity was sufficient to cover the proportions of the quantitatively important species.

Comparison between shell beds

Significant differences between shell beds are evident for faunal composition and diversities. With respect to faunal composition, shell beds C3, C4 and C5 are statistically indistinguishable for all analyses: whether absolute or relative numbers are used and for all levels of transformation there are no significant differences. These three shell beds, however, differ especially from DN2, and in all but one analysis also from C1. Shell beds DN2 and C1, finally, also differ significantly from each other. Generally the R-values, which give an absolute measure of how separated the shell beds are in the ANOSIM (analysis of similarity), are higher for relative than for absolute numbers (Table 3). This indicates that percent transformation, which considers the different sample sizes in the analyses, emphasizes the similarities within and differences between shell beds.

The results of the species richness comparison between shell beds are similar, but somewhat simpler. Only shell bed DN2 differs significantly from all other shell beds, which are conversely characterized by nearly identical species accumulation curves. This indicates that the significant differences in faunal composition between DN2 and the other shell beds are also primarily responsible for the observed differences in species abundance patterns. In contrast, the still significant but much smaller differences in faunal composition between shell bed C1 and C3 to C5 did not result in significant differences between the respective species accumulation curves. Not surprisingly therefore, the presence of significant differences in faunal composition and diversity between shell beds suggests that sampling a single shell bed at such a locality can be insufficient to characterize the local fauna and its diversity, even when sampling intensity within the shell bed was high.

Differences between shell beds could be due to numerous palaeoecological and taphonomic factors. Based on the palaeoecological and taphonomic features

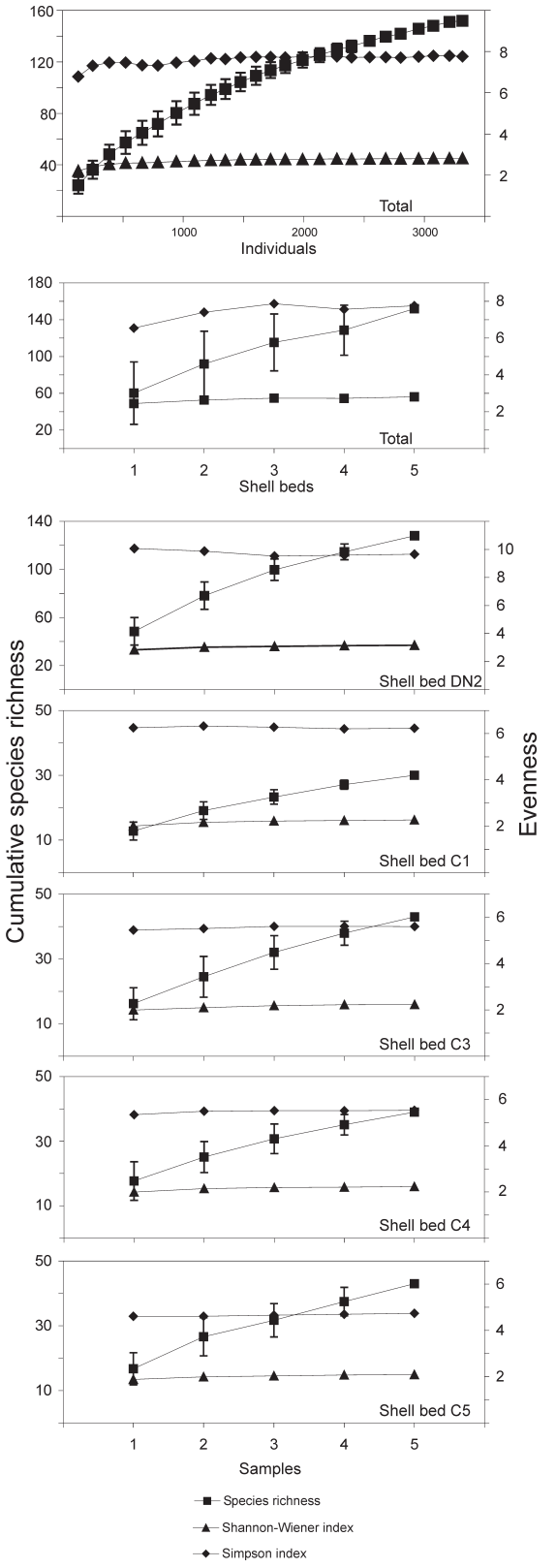

Fig. 5. Cumulative species richness and evenness (measured with the Shannon-Wiener index and the Simpson index) for the total fauna and for shell beds. For the site and shell beds, species richness does not level off, but evenness is very stable. Each point in the diversity curves is a mean value from 50 sample order randomizations without replacement (default settings of the program).

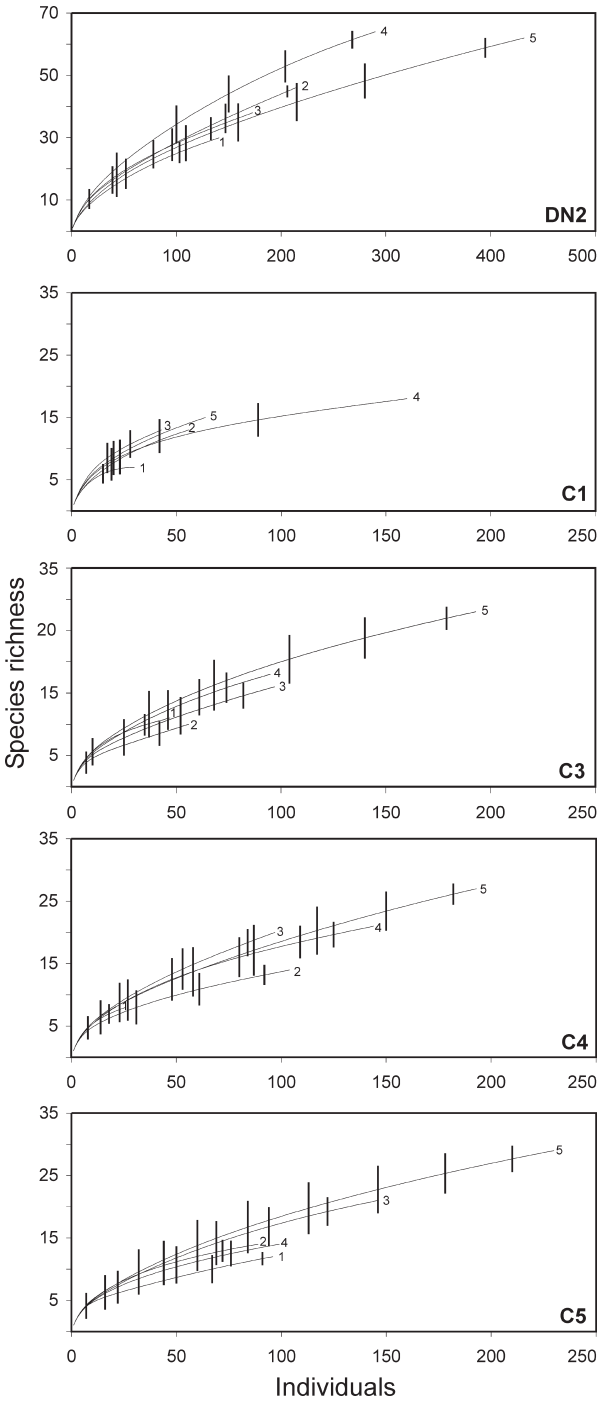

Fig. 6. Rarefaction curves with 95% confidence intervals for samples within shell beds. Rarefaction curves do not level off and are characterized by strongly overlapping confidence intervals. Exceptions are sample 4 in shell bed DN2, sample 2 in shell bed C4 and sample 1 in shell bed C5, which are characterized by comparatively steep or gentle slopes, respectively.

of the assemblages, the source area for the shells in the studied 5 skeletal concentrations is very similar. The overall high diversity, and the dominance of infaunal bivalves, *Loripes*, *Timoclea* gastropods (*Turritella*) and encrusting oysters in all shell beds, points to a mixed

Table 3. Results of ANOSIM (analysis of similarity) for shell beds with different levels of transformation. A. Absolute abundance data. B. Percentage abundance data. Bold types = 1% significance level, underlined type = 5% significance level.

shell beds	no transformation		square root transformation		fourth root transformation		presence/absence	
	R-stat	*P*-value	R-stat	*P*-value	R-stat	*P*-value	R-stat	*P*-value
A								
DN2 versus C1	0.88	**0.008**	0.892	**0.008**	0.868	**0.008**	0.868	**0.008**
DN2 versus C3	0.504	*0.016*	0.72	**0.008**	0.8	**0.008**	0.852	**0.008**
DN2 versus C4	0.464	*0.016*	0.648	**0.008**	0.748	**0.008**	0.792	**0.008**
DN2 versus C5	0.76	**0.008**	0.74	**0.008**	0.8	**0.008**	0.828	**0.008**
C1 versus C3	0.384	*0.040*	0.236	0.087	0.072	0.270	−0.028	0.563
C1 versus C4	0.458	*0.016*	0.556	*0.016*	0.58	**0.008**	0.55	**0.008**
C1 versus C5	0.492	*0.024*	0.456	*0.016*	0.408	*0.016*	0.36	*0.024*
C3 versus C4	0.044	0.286	0.08	0.167	0.096	0.151	0.136	0.119
C3 versus C5	0.224	0.063	0.136	0.135	0.072	0.286	0.008	0.468
C4 versus C5	−0.032	0.563	0.108	0.175	0.192	0.095	0.216	0.079
B								
DN2 versus C1	0.916	**0.008**	0.828	**0.008**	0.836	**0.008**	0.868	**0.008**
DN2 versus C3	0.62	**0.008**	0.7	**0.008**	0.78	**0.008**	0.852	**0.008**
DN2 versus C4	0.728	**0.008**	0.76	**0.008**	0.784	**0.008**	0.792	**0.008**
DN2 versus C5	0.864	**0.008**	0.76	**0.008**	0.812	**0.008**	0.828	**0.008**
C1 versus C3	0.84	**0.008**	0.6	*0.016*	0.224	*0.048*	−0.028	0.563
C1 versus C4	0.718	**0.008**	0.724	**0.008**	0.68	**0.008**	0.55	**0.008**
C1 versus C5	0.68	**0.008**	0.592	**0.008**	0.464	*0.016*	0.36	*0.024*
C3 versus C4	0.092	0.190	0.08	0.167	0.100	0.151	0.136	0.119
C3 versus C5	0.292	0.071	0.116	0.206	0.028	0.413	0.008	0.468
C4 versus C5	0.004	0.437	0.156	0.087	0.228	0.056	0.216	0.079

soft- and hard bottom shelf environment. Differences in the rank order of the most abundant species and differences in diversity in general could reflect ecological differences in the original environment, but could also be due to different degrees of taphonomic disintegration, habitat mixing and time-averaging of the shelly assemblage in the source area (e.g. Staff & Powell 1988; Kidwell 2002). Ubiquitous abrasion features of most shells in the skeletal concentrations can be interpreted to stem from continuous reworking by waves or currents in the source area of the tempestites (Davies *et al*. 1989; Fürsich & Oschmann 1993). Finally, different degrees of size- and shape sorting during tempestitic transport might be responsible for the observed diversity differences (e.g. Westrop 1986; Zuschin *et al*. 2005).

Patchiness within shell beds

Patchiness has been recognized at the small spatial scale of meters to tens of meters in parautochthonous deposits (e.g. Bennington 2003; Zuschin *et al*. 2004a), and some of this original patchiness can even be preserved in tempestitic assemblages (Miller 1997b). To our knowledge, patchiness at the small scale of decimetres in relatively homogenized deposits like allochthonous tempestites has not been studied before. Differences between shell beds in degree patchiness at this small scale are indicated by differences in the scatter of samples in the MDS. Samples scatter widely in shell bed DN2, but show a more narrow range in all other shell beds, especially for standardized data, which consider the different sample sizes (Fig. 7). Similarly, within shell beds, the wide scatter of the Simpson index and of the Shannon-Wiener index supports this interpretation (Table 1). Rarefaction curves show a wide scatter of slope-steepness within shell beds, albeit with largely overlapping confidence intervals. Single samples in shell beds DN2, C4 and C5, however, are distinctly outside the range of typical slope steepness and therefore also show the presence of some patchiness at this small scale. Altogether, these different lines of evidence for patchiness demonstrate that a single sample from such a shell bed is not *a priori* sufficient to characterize its faunal composition and diversity, even when the number of counted shells was high.

Local diversities from shell beds

It is reasonable that large-scale, i.e. long-term or regional to global- scale, diversity patterns (e.g. Sepkoski 1993; Crame 2000) are more robust, for example against sampling or taphonomic biases, than the finer temporal and spatial resolutions that one attempts to achieve from the fossil record (e.g. Miller & Foote 1996; Westrop & Adrain 2001). Secular changes in the composition of taphonomically-complex shell beds probably do capture real changes in the dominant paleocommunity elements

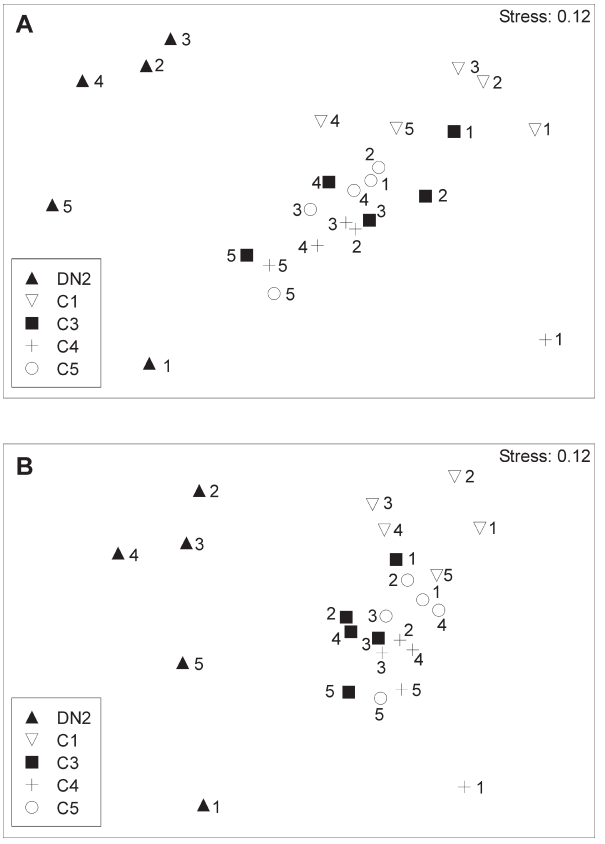

Fig. 7. Ordination of square-root transformed abundance data of fossil assemblages in the five shell beds using non-metric Multidimensional scaling (MDS). Points close to one another represent samples that are more similar in taxonomic composition than points farther away from one another. □A. Absolute abundance data. □B. Relative abundance data.

over time (e.g. Kidwell & Brenchley 1994; Copper 1997; Li & Droser 1999), whereas individual shell beds – due to their taphonomic complexity – may be unsuited to reconstruct a particular palaeocommunity (e.g. Simões & Kowalewski 1998). Comparisons of palaeoecological features, like diversity, among shell beds may therefore not be warranted, owing to differing taphonomic histories and thus different patterns or degrees of bias (Norris 1986; Kidwell 1991; Zuschin *et al*. 2005).

A related problem concerns diversity comparisons between localities. This study shows that outcrop-scale variability of faunal composition and diversity is mostly due to significant differences between shell beds, but significant patchiness can also occur within shell beds. It is therefore confirmed that sampling strategy and sampling intensity are crucial to confidently characterize the shelly assemblages at such a small spatial scale (e.g. Lafferty *et al*. 1994; Bennington 2003), and demonstrated that a dispersed sampling effort with many small replicate samples will better characterize a local assemblage or a shell bed than a few large samples (Bennington 2003).

These constraints on the quality of diversity data are important for studies that compare sample diversities between localities. This is because diversities at the larger scale must be assessed relative to the variability present at the smaller spatial scale to ensure that patterns recognized in the former are generally outside the range of variation present in the latter (Lafferty *et al*. 1994; Bennington 2003; Webber 2005). For example, the range of diversities of single samples at the outcrop-scale in this study (see Fig. 8) covers a considerable portion of the diversity range of individual samples from several localities in the Middle Miocene of the Paratethys basin (Kowalewski *et al*. 2002). Nevertheless, this study confirms the overall rather gentle slopes of diversity curves from the Miocene of the Paratethys Sea compared with such curves from the Miocene boreal bioprovince (Kowalewski *et al*. 2002). Similarly, Webber (2005) was able to demonstrate that the variability present in one outcrop in the type Cincinnatian Series (Upper Ordovician) does not significantly obscure the pattern of faunal variation at larger scales. The present study therefore confirms that broad-scale patterns are more robust than fine-scale patterns: A single sample may well be an outlier at the local scale but still be representative for faunal and diversity patterns observed at higher hierarchical levels.

Conclusion

The overriding feature of faunal assemblages at all hierarchical levels (outcrop, shell beds, samples) is the rarity of most species, which typically occur with one or two shells in only one or two samples. Nevertheless, sampling intensity in the present case study was sufficient to cover the proportions of the quantitatively important species. The four species that dominate the molluscan fauna of the outcrop are also most abundant in individual shell beds, albeit with highly variable rank orders; at the level of individual samples, other species can be important as well. This pattern most importantly results in significant differences between shell beds, and, to a lesser degree, also within shell beds (small-scale patchiness). This confirms that a dispersed sampling effort with many small replicate samples will characterize a local assemblage and its diversity better than a few large, but spatially restricted samples. The diversities of different shell beds may not be directly comparable because of differing taphonomic histories. Such comparisons are also a matter of representative sampling intensities. Diversity comparisons of individual samples between localities must ensure that patterns recognized at the larger scale (e.g. sample diversities within a basin)

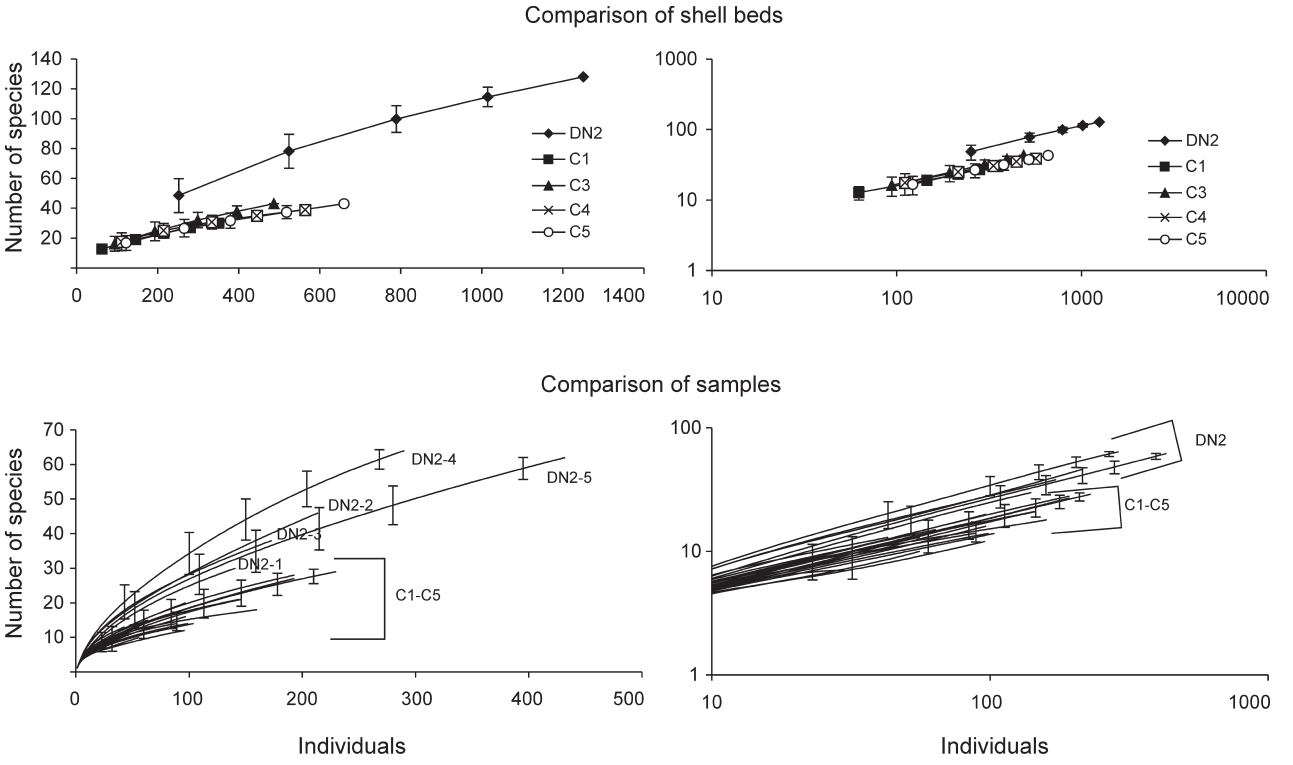

Fig. 8. Comparison of diversity curves with 95% confidence intervals between shell beds (species accumulation curves: top) and between samples (rarefaction curves: bottom) on arithmetic and logarithmic scales. Confidence intervals for rarefaction curves are only shown for selected samples.

are generally outside the range of variation at the smaller scale (i.e. sample diversities within an outcrop).

Acknowledgements. – We thank Peter Pervesler and Reinhard Roetzel for help with field work, Hubert Domanski for sample processing, Oleg Mandic for help with the identification of bivalves and Michael Stachowitsch and Johann Hohenegger for discussions. We gratefully acknowledge Susan Kidwell and Arnie Miller for insightful and constructive reviews, which improved the quality of this paper. The study was supported by project P-13745-Bio of the Austrian Science Fund (FWF).

References

Adrain, J.M. & Westrop, S.R. 2000: An empirical assessment of taxic paleobiology. *Science 289*, 110–112.

Adrain, J.M. & Westrop, S.R. 2003: Paleobiodiversity: we need new data. *Paleobiology 29*, 22–25.

Bambach, R.K. 1977: Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology 3*, 152–167.

Bennington, J.B. 2003: Transcending patchiness in the comparative analysis of palaeocommunities: a test case from the Upper Cretaceous of New Jersey. *Palaios 18*, 22–33.

Bouchet, P., Lozouet, P., Maestrati, P. & Heros, V. 2002: Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a Caledonia site. *Biological Journal of the Linnean Society 75,* 421–436.

Bray, J.R. & Curtis, J.T. 1957: An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs 27*, 325–349.

Buzas, M.A. & Hayek, L.-A.C. 2005: On richness and evenness within and between communities. *Paleobiology 31*, 199–220.

Clarke, K.R. & Gorley, R.N. 2001: *Primer v5: User Manual/Tutorial*. 91 pp. Primer-E, Plymouth.

Clarke, K.R. & Warwick, R.M. 1994: *Changes in marine communities: An approach to statistical analysis and interpretation.* 144 pp. Plymouth Marine Laboratory, Plymouth.

CoBabe, E.A. & Allmon, W.D. 1994: Effects of sampling on paleoecologic and taphonomic analyses in high-diversity fossil accumulations: an example from the Eocene Gosport Sand, Alabama. *Lethaia 27*, 167–178.

Colwell, R.K. 2000: *EstimateS: Statistical estimation of species richness and shared species from samples. Version 6.0b1 users guide and application.* Published at http://viceroy.eeb.uconn.edu/estimates.

Copper, P. 1997: Articulate brachiopod shellbeds: Silurian examples from Anticost, Eastern Canada. *Geobios, Memoires Speciaux 20*, 133–148.

Coric, S., Harzhauser, M., Hohenegger, J., Mandic, O., Pervesler, P., Roetzel, R., Rögl, F., Scholger, R., Spezzaferri, S., Stingl, K., Svabenicka, L., Zorn, I. & Zuschin, M. 2004: Stratigraphy and correlation of the Grund Formation in the Molasse Basin, northeastern Austria (Middle Miocene, Lower Badenian). *Geologica Carpathica 55*, 207–215.

Crame, J.A. 2000: Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. *Paleobiology 26*, 188–214.

Davies, D.J., Powell, E.N. & Stanton, R.J. Jr. 1989: Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. *Palaeogeography, Palaeoclimatology, Palaeoecology 72*, 317–356.

Fürsich, F.T. & Oschmann, W. 1993: Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *Journal of the Geological Society, London 150*, 169–185.

Gray, J.S. 2000: The measurement of marine species diversity with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology 250*, 23–49.

Grill, R. 1941: Stratigraphische Untersuchungen mit Hilfe von Mikrofaunen im Wiener Becken und den benachbarten Molasse-Anteilen. *Oel und Kohle 37*, 595–602.

Grill, R. 1943: Über mikropaläontologische Gliederungsmöglichkeiten im Miozän des Wiener Becken. *Mitteilungen der Reichsanstalt für Bodenforschung 6,* 33–44.

Hammer, O., Harper, D.A.T. & Ryan, P.D. 2004: *PAST-Palaeontolgical Statistics, ver 1.30*. 64 pp. Published at http://folk.uio.no/ohammer/past/

Hammer, O., Harper, D.A.T. & Ryan, P.D. 2001: PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica 4*, 9 pp. Published at http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Harzhauser, M. & Kowalke, T. 2002: Sarmatian (Late Middle Miocene) gastropod assemblages of the Central Paratethays. *Facies 46*, 57–82.

Harzhauser, M., Piller, W.E. & Steininger, F.F. 2002: Circum-Mediterranean Oligo-Miocene biogeographic evolution – the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology 183*, 103–133.

Jablonski, D. 1998: Geographic variation in the molluscan recovery from the End-Cretaceous extinction. *Science 279*, 1327–1330.

Jackson, J.B.C. & Johnson, K.G. 2001: Measuring past biodiversity. *Science 293*, 2401–2404.

Johnson, K.G. 2003: New data for old questions. *Paleobiology 29*, 19–21.

Kidwell, S.M. 1991: The stratigraphy of shell concentrations. *In* Allison, P.A. & Briggs, D.E.G. (eds): *Taphonomy: Releasing the data locked in the fossil record*, 211–290. Plenum Press, New York.

Kidwell, S.M. 2002: Time-averaged molluscan death assemblages: Palimpsets of richness, snapshots of abundance. *Geology 30*, 803–806.

Kidwell, S.M. & Brenchley, P.J. 1994: Patterns in bioclastic accumulation through the Phanerozoic: changes in input or in destruction. *Geology 22*, 1139–1143.

Kowalewski, M. & Bambach, R.K. 2003: The limits of paleontological resolution. *In* Harries, J. (ed.): *Approaches in High-Resolution Stratigraphic Paleontology*, 1–48. Kluwer Academic/Plenum Publishers, New York.

Kowalewski, M., Nebelsick, J.H., Oschmann, W., Piller, W.E. & Hoffmeister, A.P. 2002: Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe: Paleogeographic, paleoecological, and biostratigraphic implications. *Bulletin of the Geological Society of America 114*, 239–256.

Kruskal, J.B. 1964: Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika 29*, 1–27.

Lafferty, A., Miller, A.I., & Brett, C.E. 1994: Comparative spatial variability in faunal composition along two Middle Devonian paleoenvironmental gradients. *Palaios 9*, 224–236.

Lande, R. 1996: Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos 76*, 5–13.

Li, X. & Droser, M.L. 1999: Lower and Middle Ordovician shell beds from the Basin and Range Province of the western United States (California, Nevada, and Utah). *Palaios 14*, 215–233.

Li, X. & Droser, M.L. 1997: Nature and distribution of Cambrian shell concentrations: Evidence from the basin and range province of the western United States (California, Nevada, and Utah). *Palaios 12*, 111–126.

Magurran, A.E. 2004: *Measuring biological diversity*. 256 pp. Blackwell, Oxford.

Mandic, O., Harzhauser, M., Spezzaferri, S. & Zuschin, M. 2004: The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of mollusks and foraminifera. *Geobios Mémoire spécial 24*, 193–206.

Miller, A.I. 1997a: Comparative diversification dynamics among palaeocontinents during the Ordovician Radiation. *Geobios Mémoire Spécial 20*, 397–406.

Miller, A.I. 1997b: Counting fossils in a Cincinnatian storm bed: Spatial resolution in the fossil record. *In* Brett, C.E. & Baird, G.C. (eds): *Paleontological events. Stratigraphic, ecological, and evolutionary implications,* 57–72. Columbia University Press, New York.

Miller, A.I. & Foote, M. 1996: Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology 22*, 304–309.

Norris, R.D. 1986: Taphonomic gradients in shelf fossil assemblages: Pleistocene Purisma Formation, California. *Palaios 1*, 256–270.

Roetzel, R. & Pervesler, P. 2004: Storm-induced event deposits in the type area of the Grund Formation (Middle Miocene, Lower Bdenian) in the Molasse Zone of Lower Austria. *Geologica Carpathica 55*, 87–102.

Rögl, F. 1998: Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien 99A*, 279–310.

Rögl, F., Spezzaferri, S. & Coric, S. 2002: Micropaleontology and biostratigraphy of the Karpatian-Badenian transition (Early-Middle Miocene boundary) in Austria (Central Paratethys). *Courier Forschungsinstitut Senckenberg 237*, 47–67.

Sauermoser, K. 2004: Kleindimensionale räumliche Verteilung von Fossilien in tempestitischen Muschelschillen im Miozän (Unteres Badenium) von Immendorf. MS Thesis, University of Vienna, 64 pp.

Sepkoski, J.J. Jr. 1988: Alpha, beta, or gamma: where does all the diversity go? *Paleobiology 14*, 221–234.

Sepkoski, J.J.Jr. 1993: Ten years in the library: new data confirm paleontological patterns. *Paleobiology, 19*, 43–51.

Simões, M.G. & Kowalewski, M. 1998: Shell beds as Paleoecological puzzles: a case study from the Upper Permian of the Paraná Basin, Brazil. *Facies 38*, 175–196.

Steininger, F.F. & Wessely, G. 2000: From the Tethyan Ocean to the Paratethys Sea: Oligocene to Neogene Stratigraphy, Paleogeography and Paleobiogeography of the circum-Mediterranean region and the Oligocene to Neogene evolution in Austria. *Mitteilungen der Österreichischen Geologischen Gesellschaft 92*, 95–116.

Valentine J.W., 1969: Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology 12*, 684–709.

Valentine, J.W., Foin, T.C. & Peart, D. 1978: A provincial model of Phanerozoic marine diversity. *Paleobiology 4*, 55–66.

Vermeij, G.J. & Leighton, L.R. 2003: Does global diversity mean anything? *Paleobiology 29*, 3–7.

Webber, A.J. 2005: The effects of spatial patchiness on the stratigraphic signal of biotic composition (type Cincinnatian Series; Upper Ordovician). *Palaios 20*, 37–50.

Westrop, S.R. 1986: Taphonomic versus ecologic controls on taxonomic relative abundance patterns in tempestites. *Lethaia 19*, 123–132.

Westrop, S.R. & Adrain, J.M. 2001: Sampling at the species level: impact of spatial biases on diversity gradients. *Geology 29*, 903–906.

Willis, K.J. & Whittaker, R.J. 2002: Species diversity-Scale matters. *Science 295*, 1245–1248.

Zuschin, M., Harzhauser, M. & Mandic, O. 2004a: Spatial variability within a single parautochthonous Paratethyan tidal flat deposit (Karpatian, Lower Miocene Kleinebersdorf, Lower Austria). *Courier Forschungsinstitut Senckenberg 246*, 153–168.

Zuschin, M., Harzhauser, M. & Mandic, O., 2004b: Taphonomy and paleoecology of the Lower Badenian (Middle Miocene) molluscan assemblages at Grund (Lower Austria). *Geologica Carpathica 55*, 117–128.

Zuschin, M., Harzhauser, M. & Mandic, O. 2005: Influence of size-sorting on diversity estimates from tempestitic shell beds in the middle Miocene of Austria. *Palaios 20*, 142–158.

Zuschin, M. & Oliver, P.G. 2005: Diversity patterns of bivalves in a coral dominated shallow-water bay in the northern Red Sea – high species richness on a local scale. *Marine Biology Research 1*, 396–410.

Appendix

Species most responsible for dissimilarity between shell beds. For discriminating species, the ratio of average dissimilarity

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%
Average dissimilarity = 61.28	**DN2**	**C1**			
Ostrea cf. *digitalina*	14.8	20.2	11.85	2.15	19.34
Timoclea marginata	65.2	5.8	8.41	2.19	13.73
Turritella eryna	13.4	15.6	7.53	3.31	12.29
Sandbergeria perpusilla	17	4.2	3.23	1.54	5.27
Nassarius schoenni	15.2	0	2.8	2.56	4.57
Loripes dentatus	33.2	8.6	2.71	1.35	4.42
Granulolabium bicinctum	3.6	3.6	1.85	1.69	3.02
Semibittium multiliratum	8	0	1.71	1.06	2.79
Turritella bicarinata	4	2.4	1.44	1.54	2.34
Ervilia pusilla	6.8	0.4	1.11	1.68	1.82
Bittium cf. *reticulatum*	5	0.2	1.05	1.25	1.72
Gibbula buchi	0.8	0.6	0.57	1	0.94
Nassarius cerithiformis	2.8	0	0.57	1.49	0.93
Clausinella vindobonensis	4	0.4	0.56	1.23	0.92
Agapilia picta	2.4	1.2	0.56	1.11	0.91
Clausinella basteroti	1	1	0.54	1.63	0.88
Corbula carinata s.l.	2	0.8	0.44	1.36	0.72
Gouldia minima	2	0.2	0.35	1.49	0.58
Nassarius sp. 6	1.4	0	0.3	1.06	0.5
Nassarius sp. 7	1	0	0.26	1.04	0.42
Alvania sp. 1 *(?curta)*	1	0	0.23	1.03	0.38
Average dissimilarity = 47.56	**DN2**	**C3**			
Ostrea cf. *digitalina*	14.8	18.8	7.25	2.39	15.25
Loripes dentatus	33.2	25.4	6.57	2.4	13.82
Timoclea marginata	65.2	25.2	5.05	1.43	10.62
Sandbergeria perpusilla	17	1.2	2.9	1.48	6.1
Nassarius schoenni	15.2	0	2.8	2.56	5.89
Semibittium multiliratum	8	0	1.71	1.06	3.6
Turritella eryna	13.4	7.2	1.69	1.25	3.56
Bittium cf. *reticulatum*	5	0.2	1.07	1.24	2.24
Ervilia pusilla	6.8	2.4	0.77	1.32	1.61
Clausinella vindobonensis	4	2.2	0.73	1.28	1.53
Turritella bicarinata	4	1	0.67	1.3	1.4
Nassarius cerithiformis	2.8	0	0.57	1.49	1.2
Corbula carinata s.l.	2	1.8	0.56	1.57	1.19
Granulolabium bicinctum	3.6	1.4	0.56	1.4	1.17
Clausinella basteroti	1	1	0.45	1.51	0.95
Paroxystele cf. *amedei*	0.6	1	0.35	1.34	0.73
Neverita josephinia	1	0.4	0.33	1.13	0.69
Gouldia minima	2	0	0.33	1.42	0.69
Nassarius sp. 6	1.4	0	0.3	1.06	0.64
Natica tigrina	1.4	0	0.27	1.36	0.56
Nassarius sp. 7	1	0	0.26	1.04	0.54
Cardites sp. 2	0.8	0.6	0.24	1.11	0.5
Alvania sp. 1 *(?curta)*	1	0	0.23	1.03	0.49
Setia laevigata	0.8	0	0.16	1.59	0.34
Rissoina podolica	0.8	0	0.14	1.01	0.29
Average dissimilarity = 54.15	**DN2**	**C4**			
Ostrea cf. *digitalina*	14.8	30.4	9.71	2.1	17.94
Loripes dentatus	33.2	31.2	7.75	2.97	14.31
Timoclea marginata	65.2	18.2	4.72	1.31	8.72
Sandbergeria perpusilla	17	0	3.49	1.71	6.44
Nassarius schoenni	15.2	0	2.8	2.56	5.17
Semibittium multiliratum	8	0	1.71	1.06	3.16
Turritella eryna	13.4	5.6	1.7	1.51	3.13
Ervilia pusilla	6.8	3.6	1.6	1.03	2.96
Corbula carinata s.l.	2	4.8	1.34	1.3	2.47
Bittium cf. *reticulatum*	5	0	1.1	1.19	2.03
Clausinella vindobonensis	4	2.4	0.68	1.25	1.26
Nassarius cerithiformis	2.8	0	0.57	1.49	1.05
Turritella bicarinata	4	0.8	0.51	1.05	0.94
Gouldia minima	2	1.2	0.51	1.17	0.94
Natica tigrina	1.4	0.6	0.35	1.2	0.64
Nassarius sp. 6	1.4	0	0.3	1.06	0.56
Nassarius sp. 7	1	0	0.26	1.04	0.48
Cardites sp. 2	0.8	0.6	0.24	1.2	0.45
Gibbula buchi	0.8	0.8	0.24	1.51	0.44
Alvania sp. 1 *(?curta)*	1	0	0.23	1.03	0.43
Clausinella basteroti	1	0.4	0.21	1.64	0.4
Neverita josephinia	1	0	0.2	1.69	0.37
Glycymeris deshayesi	0.6	0.4	0.19	1.04	0.35
Setia laevigata	0.8	0	0.16	1.59	0.3
Average dissimilarity = 56.19	**DN2**	**C5**			
Species A					
Ostrea cf. *digitalina*	14.8	38.4	12.45	3.08	22.15
Loripes dentatus	33.2	42.4	8.27	2.35	14.72
Timoclea marginata	65.2	18	6.15	1.58	10.94
Sandbergeria perpusilla	17	1.6	3.03	1.6	5.39
Nassarius schoenni	15.2	0	2.8	2.56	4.98
Turritella eryna	13.4	8.4	2.45	1.31	4.36
Semibittium multiliratum	8	0	1.71	1.06	3.05
Bittium cf. *reticulatum*	5	0	1.1	1.19	1.95
Ervilia pusilla	6.8	1.8	0.94	1.43	1.68
Gouldia minima	2	2.4	0.74	1.14	1.32
Granulolabium bicinctum	3.6	1.6	0.74	1.32	1.32
Turritella bicarinata	4	2.4	0.64	2.35	1.15
Nassarius cerithiformis	2.8	0	0.57	1.49	1.02
Clausinella vindobonensis	4	2.6	0.53	1.68	0.94
Corbula carinata s.l.	2	1.2	0.38	1.43	0.68
cf. *Acrilla kimakowiczi*	0.2	0.8	0.34	1.25	0.6
Nassarius sp. 6	1.4	0	0.3	1.06	0.54
Natica tigrina	1.4	0	0.27	1.36	0.48
Nassarius sp. 7	1	0	0.26	1.04	0.46
Alvania sp. 1 *(?curta)*	1	0.2	0.25	1.13	0.44
Aequipecten macrotis	0.4	0.6	0.24	1.18	0.42
Cardites sp. 2	0.8	0.8	0.23	1	0.41
Paroxystele cf. *amedei*	0.6	0.6	0.21	1.13	0.37
Neverita josephinia	1	0	0.2	1.69	0.35
Gibbula buchi	0.8	0.2	0.19	1.2	0.33
Setia laevigata	0.8	0.2	0.17	1.62	0.3
Average dissimilarity = 45.91	**C1**	**C3**			
Timoclea marginata	5.8	25.2	8.31	1.68	18.09
Loripes dentatus	8.6	25.4	7.18	2.15	15.64
Turritella eryna	15.6	7.2	6.51	4.29	14.17
Ostrea cf. *digitalina*	20.2	18.8	5.81	1.27	12.66
Granulolabium bicinctum	3.6	1.4	1.97	1.74	4.29
Turritella bicarinata	2.4	1	1.41	1.49	3.07
Ervilia pusilla	0.4	2.4	0.98	1.46	2.13
Clausinella vindobonensis	0.4	2.2	0.95	1.45	2.07
Corbula carinata s.l.	0.8	1.8	0.64	1.42	1.39
Gibbula buchi	0.6	0.4	0.59	1.01	1.29
Clausinella basteroti	1	1	0.52	1.24	1.13
Paroxystele cf. *amedei*	0.2	1	0.35	1.22	0.77
Average dissimilarity = 48.73	**C1**	**C4**			
Loripes dentatus	8.6	31.2	8.36	2.59	17.15
Turritella eryna	15.6	5.6	7.55	4.5	15.5
Ostrea cf. *digitalina*	20.2	30.4	7.12	1.29	14.6
Timoclea marginata	5.8	18.2	4.36	1.8	8.94
Ervilia pusilla	0.4	3.6	2.18	1.18	4.47
Granulolabium bicinctum	3.6	2.6	1.94	1.59	3.99
Turritella bicarinata	2.4	0.8	1.66	1.83	3.41
Corbula carinata s.l.	0.8	4.8	1.4	1.27	2.87
Clausinella vindobonensis	0.4	2.4	0.74	1.12	1.51
Gibbula buchi	0.6	0.8	0.61	1.43	1.25
Clausinella basteroti	1	0.4	0.54	1.36	1.11
Average dissimilarity = 56.19	**C1**	**C5**			
Species A					
Ostrea cf. *digitalina*	14.8	38.4	12.45	3.08	22.15
Loripes dentatus	33.2	42.4	8.27	2.35	14.72
Timoclea marginata	65.2	18	6.15	1.58	10.94
Sandbergeria perpusilla	17	1.6	3.03	1.6	5.39
Nassarius schoenni	15.2	0	2.8	2.56	4.98
Turritella eryna	13.4	8.4	2.45	1.31	4.36
Semibittium multiliratum	8	0	1.71	1.06	3.05
Bittium cf. *reticulatum*	5	0	1.1	1.19	1.95
Ervilia pusilla	6.8	1.8	0.94	1.43	1.68
Gouldia minima	2	2.4	0.74	1.14	1.32
Granulolabium bicinctum	3.6	1.6	0.74	1.32	1.32
Turritella bicarinata	4	2.4	0.64	2.35	1.15
Nassarius cerithiformis	2.8	0	0.57	1.49	1.02
Clausinella vindobonensis	4	2.6	0.53	1.68	0.94
Corbula carinata s.l.	2	1.2	0.38	1.43	0.68
cf. *Acrilla kimakowiczi*	0.2	0.8	0.34	1.25	0.6
Nassarius sp. 6	1.4	0	0.3	1.06	0.54
Natica tigrina	1.4	0	0.27	1.36	0.48
Nassarius sp. 7	1	0	0.26	1.04	0.46
Alvania sp. 1 *(?curta)*	1	0.2	0.25	1.13	0.44
Aequipecten macrotis	0.4	0.6	0.24	1.18	0.42
Cardites sp. 2	0.8	0.8	0.23	1	0.41
Paroxystele cf. *amedei*	0.6	0.6	0.21	1.13	0.37
Neverita josephinia	1	0	0.2	1.69	0.35
Gibbula buchi	0.8	0.2	0.19	1.2	0.33
Setia laevigata	0.8	0.2	0.17	1.62	0.3

Supplementary material, Online Data Set, is available in the online version of this paper (www.tandf.no/leth).