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Linking taphonomy to community-level abundance: Insights into compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps)

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Abstract

Although actualistic live/dead comparisons lead to robust estimates of fidelity of modern death assemblages, quantitative evaluation of fidelity of fossil assemblage remains uncertain. In this paper, effects of storm reworking on compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps, Austria) are evaluated. An exploratory approach is based on comparison of reworked and non-reworked assemblages in ordination analyses. Non-reworked assemblages of one or more communities provide a baseline for evaluation of fidelity of reworked assemblages. In siliciclastic-rich intervals of the Kössen Formation, shell concentrations are represented by (1) packstones with small, shallow infaunal bivalves, (2) floatstones and pavements with large semi-infaunal bivalves, and (3) bioclastic marlstones. In carbonate-rich intervals, bioclastic floatstones with bivalves and brachiopods occur. Analyzing all shell concentrations, eight sample groups sharing similar species composition are discriminated. Limited effect of storm reworking on composition of shell concentrations is indicated by (1) a general persistence of six sample groups when only non-reworked assemblages are analyzed, (2) similarity in composition between reworked and non-reworked assemblages within sample groups, and (3) compositional segregation between non-reworked assemblages of distinctive sample groups, mostly without any reworked assemblages of intermediate composition.

Depth-related variations in dead-shell production, shell destruction and body size governed preservation and distribution of the shell concentrations along onshore-offshore gradient in the Kössen Basin. First, at times when environmental conditions were unfavorable for shell producers, coupled with high background shell destruction rates, limestone beds formed during storm events were shell-poor. Second, less common shell concentrations in upper than in lower parts of siliciclastic intervals can be related to higher environmental stress in shallower habitats. Third, the difference between shell concentrations dominated by small and large bivalves is driven by between-habitat differences in body size and is not due to a differential sorting of small and large shells. Combining community analysis based on species abundances with taphonomic analysis can thus be helpful in tracking fidelity of fossil assemblages.

Keywords: Triassic; Eastern Alps; Taphonomy; Paleoecology; Shell concentration; Storm-reworking; Bivalve; Brachiopod

1. Introduction

Taphonomic analyses are either used for (1) interpreting environmental gradients (Brett and Baird, 1986; Davies et al., 1989; Feige and Fürsich, 1991; Kowa-

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lewski et al., 1994; Nebelsick, 1999; Dominici, 2004; Parsons-Hubbard, 2005), or (2) as a tool for addressing questions related to fidelity of the fossil record (Kidwell and Flessa, 1995; Behrensmeyer et al., 2000). The latter point leads to a choice of which fossil assemblages are minimally affected by compositional bias. Such assemblages can be suitable for further ecologic and environmental analyses. However, in spite of a large amount of research (Johnson, 1960; Miller, 1988; Powell et al., 1989; Kidwell and Bosence, 1991; Kidwell, 2001; Zuschin et al., 2004), quantitative estimation of effects of reworking on fidelity of fossil assemblages still remains uncertain because the original biologic pattern of interest is not controlled (in contrast to actualistic fidelity studies).

If fossil assemblages that show some evidence of reworking are excluded (see Johnson, 1960; Kidwell, 1998), the analyzed patterns in biotic composition should not be artifacts of sorting and mixing. However, some shallow, high-energy habitats are preferentially affected by higher physical destruction rates and transport. If such habitats harbor unique benthic communities, they will be excluded from the analyses due to their poor preservation. Some parts of the environmental gradient will not be analyzed due to such exclusion. High destruction rates can also be typical of some low energy habitats where chemical or biologic destructive processes are very rapid. Episodic short-term reworking events, associated with rapid burial, can lead to better preservation potential in such habitats. Paradoxically, such reworking can produce signs of sorting and transport, possibly also leading to the exclusion of such assemblages from paleoecologic analyses. Clearly, the ability to estimate what and how much of original information was lost during reworking events is crucial in paleoecologic analyses.

The compositional fidelity (i.e., the quantitative faithfulness of the population- and community-level fossil/subfossil data to the original biologic record, Behrensmeyer et al., 2000) can be explicitly assessed in actualistic live–dead studies where original biologic record is available (Schopf, 1978; Nebelsick, 1992; Greenstein, 1993; Murray and Alve, 1999; Hadly, 1999; Zuschin et al., 2000; Kidwell, 2001, 2002; Alin and Cohen, 2004; Tomašových, 2004). However, the direct live/dead comparison is not possible in fossil assemblages. Several indirect measures can be used when the compositional fidelity of fossil assemblages is evaluated. These measures are based mostly on an overall degree of fossil damage and/or sedimentologic evidence for reworking, transport or condensation (Kidwell and Bosence, 1991; Jiménez and Braga, 1993; Olszewski and West, 1997; Yesares-García and Aguirre, 2005; Cózar, 2002). However, sedimentologic and taphonomic evidence indicating reworking does not tell if and to what degree an original biotic pattern of interest (e.g., species composition, abundances or diversity) is preserved in the fossil assemblage affected by the reworking. For example, Rasser and Nebelsick (2003) showed that Oligocene foraminiferal assemblages preserved in debris flows may well reflect composition of their autochthonous counterparts.

One of the few attempts to quantitatively analyze compositional fidelity which would be applicable to fossil assemblages is an evaluation of within-community transport (Cummins et al., 1986; Miller and Cummins, 1990). Based on the comparisons of observed number of co-occurring species pairs based on field data and predicted number of co-occurring species pairs based on simulation, Cummins et al. (1986) and Miller and Cummins (1990) showed that Spearman rank correlation coefficient can be a viable measure for discerning transport within habitats.

In this paper, an explorative approach is proposed for assessment of the compositional fidelity of fossil assemblages. This method is based on a simple comparison of the composition of reworked and non-reworked assemblages, assuming that they are derived from comparable habitats and time intervals (e.g., are assemblages affected by higher reworking different in composition compared to non-disturbed assemblages?). The relationship of reworked and non-reworked assemblages in Q-mode ordination space should permit inferences on the role of sorting or mixing processes in biasing the composition of fossil assemblages. The main goal of this paper is to apply this explorative approach to the Upper Triassic shell concentrations of the Kössen Formation (Eastern Alps, Austria, Fig. 1). As an initial hypothesis, Golebiowski (1990) assumed that a difference in composition between assemblages dominated by small and large bivalves in the Kössen Formation is due to storm sorting. This hypothesis will be tested and the genesis of shell concentrations from the Kössen Formation will be addressed in general. Although spatial fidelity is also of ecologic importance (e.g., Fürsich and Flessa, 1987; Miller, 1988), the focus in this paper is on the fidelity of taxonomic composition. Effects of time-averaging as another potential biasing factor on community-level properties (Meldahl et al., 1997; Kowalewski et al., 1998) are minimized as the focus is mostly on single-event shell concentrations.

In the first section, shell concentrations are described and interpreted. In the second section, their compositional fidelity is evaluated in multivariate analyses via

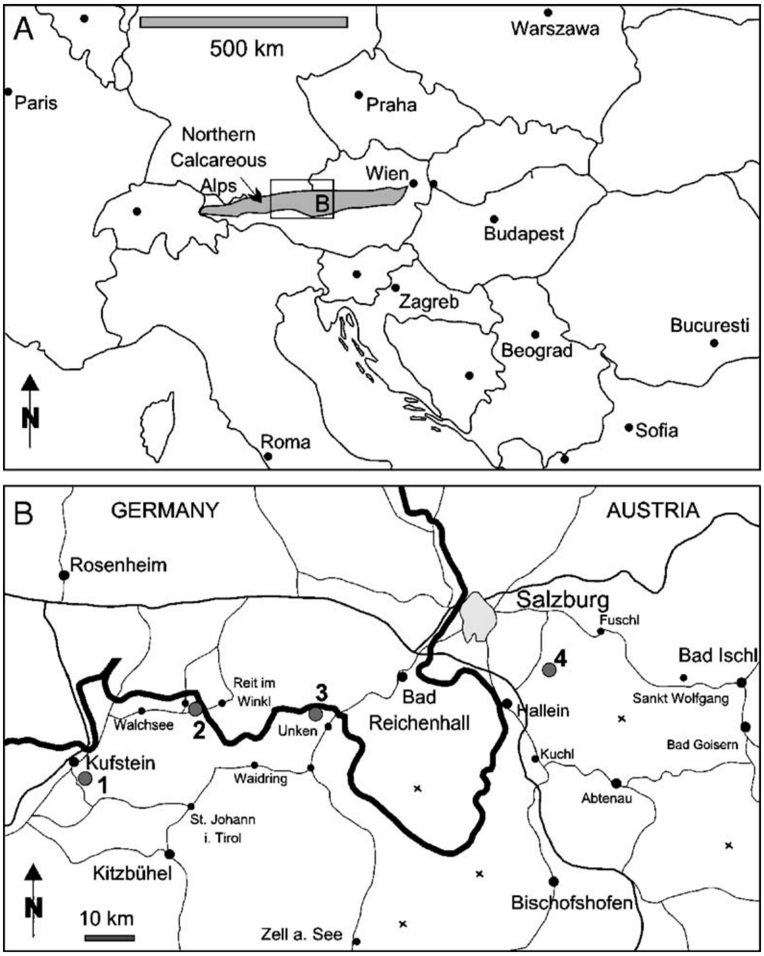


Fig. 1. Geographic location of four sections of the Kössen Formation in the Eastern Alps. 1. Eiberg. 2. Kössen. 3. Hochalm. 4. Gaissau.

comparison of reworked and non-reworked shell concentrations, supplemented by size–frequency distributions and right–left valve ratio. In the third section, some atypical features in the onshore–offshore distribution of shell concentrations from the Kössen Formation are discussed in the light of taphonomic and fidelity interpretations.

2. Geologic setting

In the Late Triassic, the Kössen Formation was deposited in an intra-platform, mixed siliciclastic-carbonate setting, separated from the open ocean by the Dachstein carbonate platform (Kuss, 1983; Golebiowski, 1990, 1991; Stanton and Flügel, 1995, McRoberts et al., 1997; Kern and Hüssner, 1997; Holstein, 2004). The Kössen Formation consists of the Hochalm Member (Lower Rhaetian) and the Eiberg Member (Upper Rhaetian; Fig. 2). The Hochalm Member is composed of small-scale sequences that consist of the siliciclastic and carbonate intervals with shell concentrations, and reflect depths mostly not exceeding maximum storm wave base (Figs. 3 and 4). The deposits of the Hochalm Member reflect a deepening-upward trend, with a maximum deepening event recorded by extensive marls that onlap on the carbonate platform (Golebiowski, 1991; Satterley, 1996). Deposits of the Eiberg Member reflect depths below maximum storm wave base. Each of these two members consists of four informal lithostratigraphic units (Golebiowski, 1990). The shell concentrations analyzed in this paper are restricted to upper parts of the Hochalm Member, including units 2–4.

3. Methods

The data about thickness, biofabric, geometry and internal structure of shell concentrations were collected in four sections (Fig. 1, Hochalm, Gaissau, Kössen, Eiberg). Absolute abundances of bivalves and brachio-

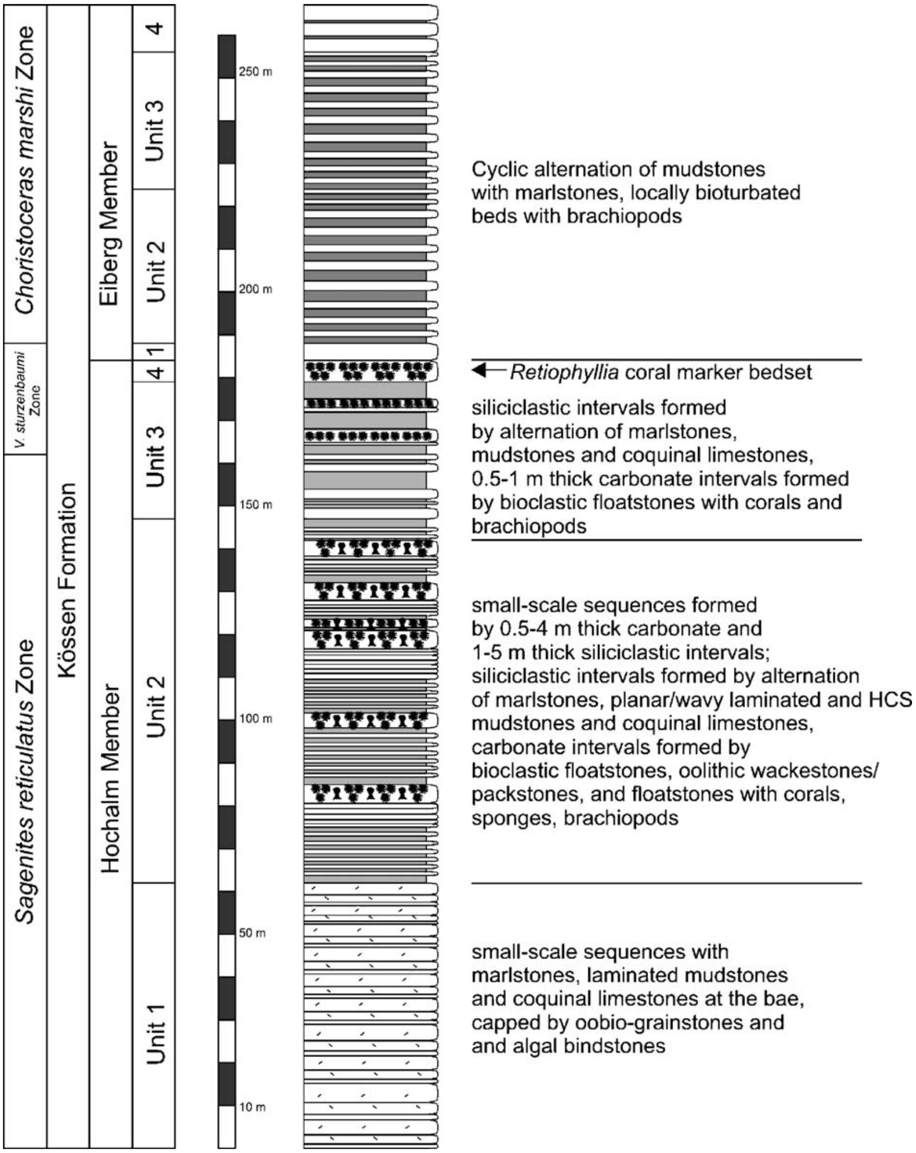


Fig. 2. Schematic section showing lithostratigraphic subdivision of the Kössen Formation according to Golebiowski (1990). Thickness is based on the Hochalm section.

pods were counted in 49 shell concentrations from units 2, 3 and 4 of the Hochalm Member (four shell concentrations are used from Golebiowski, 1989). Proportion of fragmentation was estimated by counting all fragmented specimens on bedding planes. The absolute abundances counted using the minimum number of individuals (MNI) approach (i.e., the sum of articulated shells plus dominating number of either left or right valves; Gilinsky and Bennington, 1994) were converted to relative abundances. These were transformed by the square root in order to decrease an effect of highly dominant species. In the following, the term fossil assemblage refers to any group of fossils derived from a geographic locality (Fürsich, 1990). The shell concentration is a fossil assemblage with loosely or densely packed fossils exceeding 2 mm in size. The sample group refers to samples with similar species composition discriminated by a cluster analysis. The community refers to one or more sample groups which show recurrence in biotic composition and reflect presumably the unbiased composition of original life assemblages (i.e., comparable to community type of Bambach and Bennington, 1996).

A Q-mode cluster analysis of all samples based on the Bray–Curtis similarity is used for initial discrimination of sample groups which share similar species

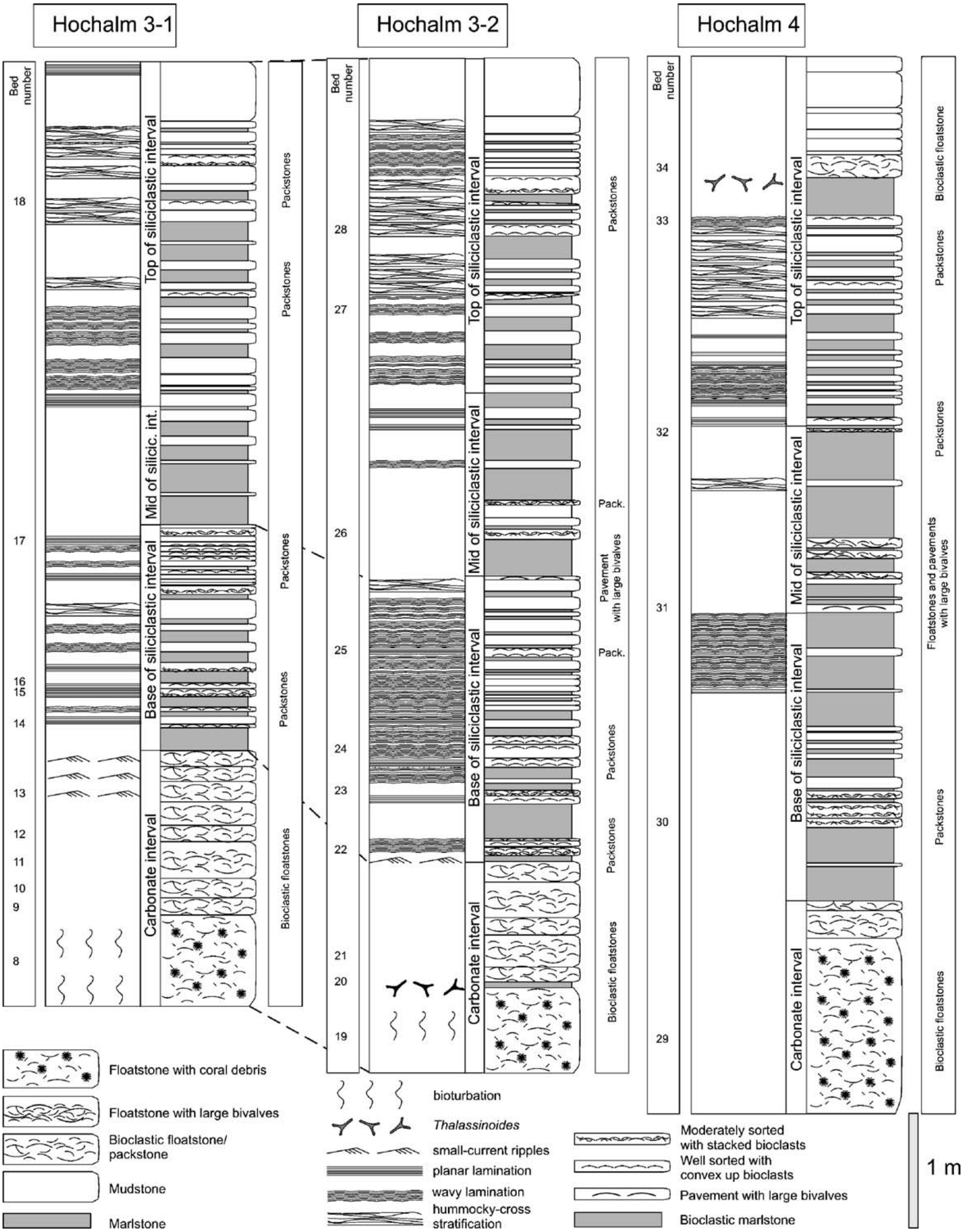


Fig. 3. Distribution of shell concentration types within two small-scale sequences in Unit 2 of the Hochalm Member. The sections Hochalm 3-1 and Hochalm 3-2 show horizontal variation in sedimentologic and taphonomic features within the same small-scale sequence. The section Hochalm 4 follows overlies this sequence. Note that shell beds in the upper parts of the siliciclastic intervals are less common in contrast to the lower parts.

composition and relative abundances. Non-metric multi-dimensional scaling (NMDS) is used as a dimension-reduction, distance-based method that effectively reduces multi-dimensional space into low-dimensional ordination space (Kenkel and Orlóci, 1986; Minchin, 1987). NMDS is here based on the rank, Bray–Curtis

Fig. 4. Distribution of shell concentration types within 3 small-scale sequences in Unit 3 of the Hochalm Member. All sections represent the equivalent stratigraphic interval. For legend, see Fig. 3.

dissimilarity matrix. NMDS has a simple concept, leading to a sample map whose inter-sample distances have the same rank order as the corresponding dissimilarities between samples (Clarke and Warwick, 2001). In order to compare reworked and non-reworked assemblages, NMDS is preferable because it does not make any assumptions about the form of the data or the interrelationship of assemblages. Although comparison of

Table 1
Characteristic taphonomic features of five shell concentration types

Shell concentration properties	Packstones	Floatstones with large bivalves	Pavements with large bivalves	Bioclastic marlstones	Bioclastic floatstones
Packing	Dense	Loose/dense	Loose	Dispersed/loose	Loose/dense
Sorting	Good/moderate	Moderate/poor	Good/moderate/poor	Poor	Moderate/poor
Orientation	Convex up-stacked	Convex up/stacked	Convex up	Random/concordant	Random/stacked
Geometry	Bed/lense/pavement	Bed/lense	Pavement	Bed	Bed
Internal structure	Simple	Simple	Simple	Simple	Complex
Fragmentation	10%	20%	10%	10%	30%
Disarticulation	High	High	High	High/moderate	Moderate

reworked and non-reworked fossil assemblages is not directly comparable to live/dead comparisons of modern assemblages, NMDS has already been used in actualistic fidelity studies (Springer and Flessa, 1996; Pandolfi and Minchin, 1995; Pandolfi and Greenstein, 1997; Zuschin et al., 2000; Edinger et al., 2001).

If possible, the difference in composition between reworked and non-reworked assemblages is tested with analysis of similarities (ANOSIM, Clarke and Green, 1988; Gray et al., 1988; Warwick and Clarke, 1991). ANOSIM is a non-parametric permutation test which is applied to the Q-mode, rank-order Bray

Table 2
Summary of species composition/relative abundances of eight sample groups (species above 1% are shown)

Sample group	Species	%	Sample group	Species	%
Isocyprina group	*Isocyprina alpina*	59.5	*Bakevellia* group	*Bakevellia praecursor*	71.0
	Bakevellia praecursor	23.0		*Rhaetavicula contorta*	18.6
	Nuculana claviformis	11.5		*Pseudocorbula ewaldi*	3.8
	Gervillaria inflata	3.2		*Myophoriopis isoceles*	2.0
	Placunopsis alpina	1.9		*Antiquilima alpis*	2.0
Cassianella group	*Cassianella inaequiradiata*	74.9	*Gervillaria* group	*Gervillaria inflata*	82.7
	Myophoriopis isoceles	10.8		*Palaeocardita austriaca*	5.6
	Protocardia rhaetica	8.5		*Placunopsis alpina*	3.5
	Placunopsis alpina	1.4		*Modiolus minutus*	2.8
	Zeilleria sp.	1.4		*Liostrea hinnities*	2.6
	Rhaetavicula contorta	1.4		*Isocyprina alpina*	1.2
	Pseudocorbula ewaldi	1.1			
Myophoriopis group	*Myophoriopis isoceles*	29.1	*Chlamys* group	*Chlamys coronata*	34.3
	Rhaetavicula contorta	27.1		*Rhaetavicula contorta*	22.8
	Protocardia rhaetica	10.6		*Protocardia rhaetica*	13.8
	Gervillaria inflata	7.5		*Homomya lagenalis*	10.3
	Placunopsis alpina	6.9		*Inoperna schafhaeutli*	3.6
	Pseudocorbula ewaldi	6.3		*Placunopsis alpina*	3.6
	Atreta intusstriata	2.8		*Pinna* sp.	3.5
	Nuculana claviformis	1.7		*Atreta intusstriata*	2.9
	Isocyprina alpina	1.7		*Entolium* sp.	2.4
	Parallelodon sp.	1.4		*Plagiostoma punctatum*	1.7
	Bakevellia praecursor	1.3		*Chlamys* sp.	1.2
R. pyriformis group	*Rhaetina pyriformis*	27.5	*R. gregaria* group	*Rhaetina gregaria*	44.3
	Zeilleria sp.	17.1		*Atreta intusstriata*	28.9
	Chlamys sp.	13.4		*Rhaetavicula contorta*	6.1
	Plagiostoma punctatum	7.2		*Gervillaria inflata*	5.7
	Rhaetina gregaria	5.2		*Palaeocardita austriaca*	3.0
	Gervillaria inflata	4.0		*Liostrea hinnities*	2.9
	Atreta intusstriata	3.5		*Chlamys* sp.	2.0
	Actinostreon haidingerianum	3.3		*Gruenewaldia inflata*	1.7
	Austrirhynchia cornigera	2.8		*Myophoriopis isoceles*	1.4
	Zugmayerella uncinata	2.7			
	Fissirhynchia fissicostata	2.6			
	Cassianella inaequiradiata	2.0			
	Modiolus minutus	1.6			
	Mysidioptera waageni	1.0			

Curtis dissimilarity matrix. It is thus conceptually linked with NMDS. The null hypothesis is that the average of pairwise rank dissimilarities within reworked or non-reworked assemblages is not lower than the average of pairwise rank dissimilarities between reworked and non-reworked assemblages. The test statistic (R) ranges from -1 to 1 and is approximately zero if the null hypothesis is true. Significance levels are computed with a general randomization Monte Carlo approach.

4. Shell concentrations

Based on deposit-level sedimentologic properties, five shell concentrations are distinguished (Table 1). They include (1) packstones with small shells (mostly

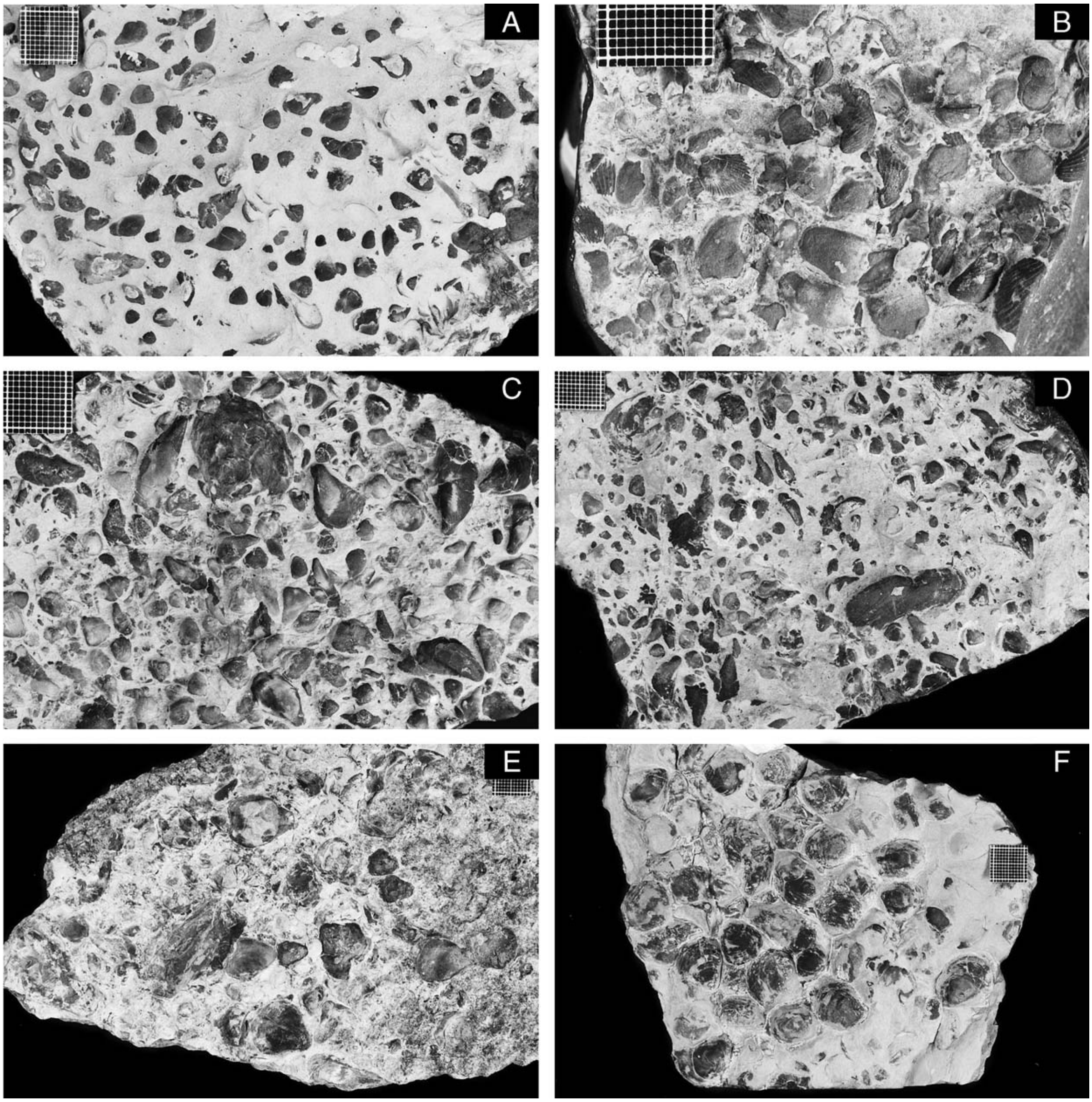


Fig. 5. Packstones (plane-views). (A) Pavement at the top of moderately sorted packstone, with abundant convex up oriented *Isocyprina*, *Bakevellia* and *Nuculana*. Sample H6. (B) Well sorted packstone with convex up oriented *Myophoriopis* and *Rhaetavicula*. Sample H18. (C–D) Loosely/densely packed pavements at the top of thin packstone, with abundant convex up oriented *Bakevellia* and *Isocyprina*. Sample K2. (E) Basal bedding plane of moderately sorted packstone with disarticulated *Rhaetina* and *Gervillaria*. Sample H4. (F) Thin pavement with convex up *Rhaetina* at the top of moderately sorted packstone. Sample K1.

bivalves, around 2–15 mm in size), (2) floatstones with large bivalves, (3) pavements with large bivalves (3–10 cm long bivalves, predominantly *Gervillaria*), (4) bioclastic marlstones and (5) bioclastic floatstones. Note that this classification is not based on shell-specific taphonomic variables (i.e., disarticulation, fragmentation etc.). The first four shell concentrations are restricted to the siliciclastic intervals and the fifth type to the carbonate intervals of the small-scale sequences. The cluster analysis of shell concentrations (not shown) based on relative abundances of species discriminates eight sample groups with similar composition (Table 2).

4.1. Packstones with convex up or stacked bioclasts

Two subtypes are recognized, including (1) well sorted packstones with convex-up oriented bioclasts (up to 5–10 mm), with a sharp but planar base (Fig. 5B–D), and (2) moderately sorted packstones with stacked, nested or edgewise-oriented bioclasts (up to 2–3 cm) and with an irregular, erosional base. Moderately sorted packstones can be capped by pavement formed by convex up-oriented valves (Fig. 5A). In spite of dense packing and rarity of articulated shells, the proportion of fragmented valves is below 10%. The bioclasts are size-graded, rarely encrusted or bored. In thin-sections, recrystallized, originally aragonitic bioclasts can show irregular changes in shell thickness and/or laterally pass into fossil ghosts that are recognizable only as very thin calcitic fibres. Packstones locally fill *Thalassinoides* burrows. Well-sorted and moderately sorted packstones can laterally replace each other and can alternate as multiple layers within planar or wavy laminated mudstones. The *Isocyprina* and *Rhaetina gregaria* sample groups (Fig. 5E–F) consistently occur in the basal portions of the siliciclastic intervals in Unit 2. In Unit 3, the *Myophoriopis* sample group occurs mostly at the base of the siliciclastic intervals or in the carbonate intervals, rarely in the middle part of the siliciclastic intervals. Some packstones can occur in the upper part of the siliciclastic intervals, but these are formed by indeterminable shell debris.

4.2. Floatstones with large bivalves

Poorly or moderately sorted and loosely packed, locally densely packed beds contain stacked or nested

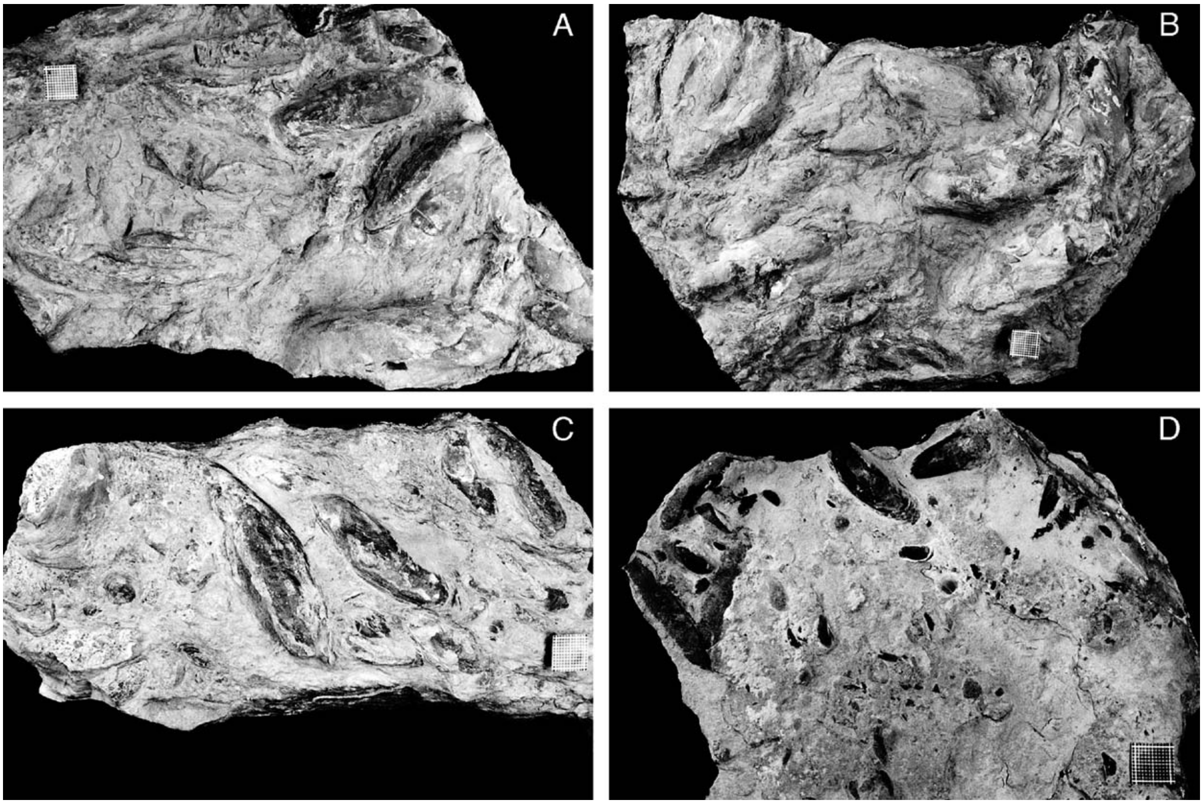


Fig. 6. Floatstones and pavements with large bivalves (plane-views). (A–B) Bedding planes of floatstone with *Gervillaria*. Sample H11. (C) Pavement with loosely packed left valves of *Gervillaria*. Sample H16. (D) Pavement with dispersed *Gervillaria* left valves. Sample H17.

large bivalves (*Gervillaria*). Floatstones can be capped by thin pavements with concordantly oriented valves (Fig. 6A–B). Both complete and fragmented valves (around 20%) are present. Disarticulated valves prevail, but articulated shells are also preserved. These beds alternate with marlstones or laminated mudstones.

4.3. Pavements with large bivalves

Mostly one- or two-valve thick, loosely packed pavements are characterized by convex-up oriented bivalves, locally sheltering fine bioclastic debris (1–2 mm in size). The sorting ranges from very good, with one size class, to moderate or poor, including both juveniles and adults. Pavements occur as thin layers within millimeter-scale wavy or ripple laminated mudstones, or they cap thin mudstones. The proportion of fragments is below 10%. In plane view, the valves are either oriented with the longest axis in parallel orientation (Fig. 6C), or are randomly oriented (Fig. 6D). Both floatstones and pavements with large bivalves contain the *Gervillaria* sample group which uniformly occurs in the middle and upper parts of the siliciclastic intervals in Units 2 and 3.

4.4. Bioclastic marlstones

Marlstones of the Hochalm Member contain mostly no or very rare macrofossils. However, in the lower parts of the siliciclastic intervals of Unit 3, marlstones locally contain densely packed and poorly sorted concentrations of bivalves (*Myophoriopis* sample group). Marlstones are several centimeters thick and locally contain multiple superimposed pavements. Complete valves dominate (above 90%). No traces of bioerosion or encrustation have been observed. Articulated shells are rare (Fig. 7A–B). In Sample H20, articulated shells of *Gervillaria* dominate in several decimeter wide clusters. Marlstones in the upper parts of Unit 3 contain mostly dispersed or loosely packed, poorly sorted and randomly oriented bivalves of the *Chlamys* and *Cassianella* sample groups.

4.5. Bioclastic floatstones

Two subtypes restricted to the carbonate intervals are dominated either by infaunal and epifaunal bivalves, or terebratulid brachiopods. The first subtype is formed by 10–50 cm thick floatstones, less commonly packstones, with randomly oriented, loosely packed and poorly/

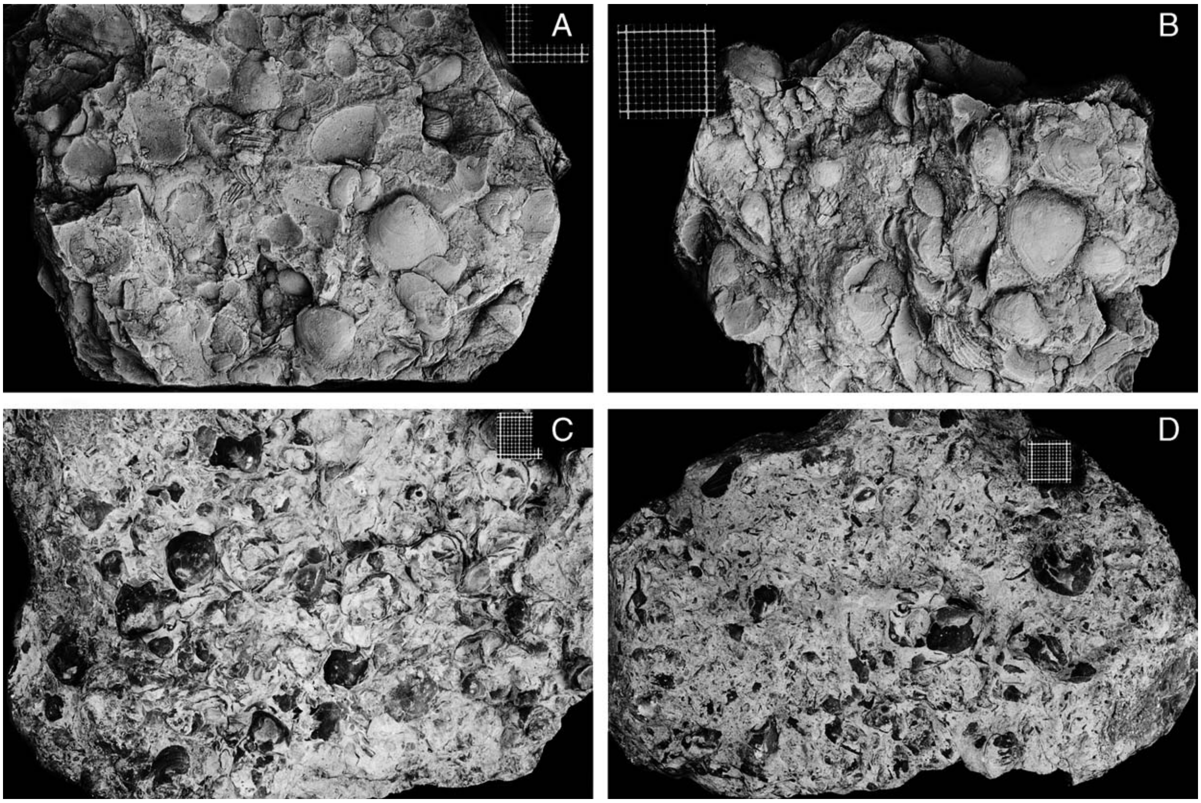


Fig. 7. Bioclastic floatstones (plane-views). (A–B) Bioclastic marlstone with concentrations of disarticulated but mostly complete bivalves *Myophoriopis* and *Protocardia*. Sample E10. (C–D) Bioclastic floatstone with disarticulated, commonly stacked valves of *Rhaetina gregaria*. Sample H3.

moderately sorted disarticulated bivalve fragments. Packstones show moderate/good sorting and concordantly oriented bivalves. The proportion of fragmented valves is mostly higher than 30%. Bivalves are commonly covered with micritic crusts, encrusted and bored. Similarly, as in packstones in the siliciclastic intervals, some bioclasts show signs of partial thinning or complete removal of shell wall in thin-sections. Locally, articulated bivalves are thus represented by internal moulds with sediment infill that slightly differs from a surrounding matrix (e.g., Sanders, 2003). Micritic intraclasts, ooids and peloids are locally present. This subtype contains the *Myophoriopis* sample group. The second subtype is represented by poorly sorted, bioturbated brachiopod floatstones, locally with internal stratification. Brachiopods are dispersed or loosely packed (Fig. 7C–D). Articulated, randomly oriented shells may dominate or stacked/edgewise disarticulated valves can be also abundant. The external and internal valve surfaces of bioclasts can be encrusted, bored or covered with micritic crusts. This subtype contains the *Rhaetina gregaria* and *R. pyriformis* sample groups.

5. Genesis of shell concentrations

5.1. Packstones

Sharp planar or irregular erosional bases, micritic matrix and low proportions of fragmentation point to short-term episodic storm-reworking. Pristine preservation indicates either very short residence time and/or low rate of shell destruction. Fossil ghosts represent shell relicts that were partly dissolved during organic matter oxidation and sulphate reduction within sediment (Sanders, 2003). Convex-up valves indicate storm-flow conditions, stacked/edgewise positions more turbulent conditions, around normal storm wave base or above maximum storm wave base. Small-scale vertical and/or horizontal replacements between well- and moderately sorted packstones indicate that their deposition took place in equivalent depths. The presence of pre-depositional traces filled with shells indicates that storm erosion cut down to levels of moderately firm sediment.

5.2. Floatstones and pavements with large bivalves

Spatial association of floatstones with large bivalves with erosional surfaces, their restricted geometry and stacked shell orientations indicate short-term episodic reworking. Thin pavements with convex-up valves in the uppermost parts indicate a change from a turbulent to a laminar hydrodynamic regime, probably related to storm waning. However, poor sorting, high proportion of micritic matrix, and local presence of articulated shells indicate no substantial intensity of reworking (i.e., more or less in situ storm-wave reworking coupled with rapid burial). Pavements with large bivalves are mostly better sorted and preferred valve orientations suggest unidirectional current activity (Golebiowski, 1989). Shell-shelters indicate that the smallest size classes (1–2 mm in size), if present, were mostly winnowed and transported out of habitat. Both pavements with large bivalves and packstones are dominated by semi-infaunal or infaunal bivalves. Therefore, their position on the top of laminated or HCS bed indicates that the winnowing and exhumation of bivalves out of substrate preceded their deposition during storm events (see Aigner, 1977 for analogous origin of shell pavements in the Triassic Hauptmuschelkalk). The pavements can thus be related to exhumation of bivalves followed by storm-flow deposition.

5.3. Bioclastic marlstones

If it is assumed that high shell density in single-event beds is due to winnowing from marls, some shells should be dispersed in marlstones. However, packstones are typically embedded between barren marlstones or mudstones. Bioclastic marlstones are rather an exception to this pattern. The signs of dissolution in packstones can indicate that the fine-grained sediment was probably undersaturated with respect to calcium carbonate. Low levels of fragmentation or bioerosion observed in bioclastic marlstones can thus indicate short residence times, possibly coupled with high destruction rates via shell dissolution. A rate of shell destruction was probably decreased during episodic storm events. Therefore, although background sedimentation rates were probably not high, passive concentration of shells due to the lack of sediment dilution did not take place. Dead-shell production rates probably surpassed destruction rates only at times of high shell input, either due to high fertility or catastrophic mortality. High rate of dead-shell production was thus necessary for origin of shell-rich marlstones. Alternatively, as some bioclastic marlstones are composed of stacked pavements of disarticulated shallow infaunal bivalves, fine distal storm winnowing with no trace of substantial erosion or transport could be responsible for the shell enrichment. Bioclastic marlstones probably reflect depths near or below maximum storm wave base.

Storm events could lead either to (1) rapid burial or (2) secondary concentration of shells by exhumation and matrix winnowing. The first process can reduce the rate of shell destruction due to shorter residence time. The second process can also lead to a decrease in rate of shell destruction because of various density-dependent effects of high shell density during early diagenesis (e.g., favorable early diagenetic microenvironment, Kidwell, 1986). In both cases, conditions for enhanced preservation were produced.

5.4. Bioclastic floatstones

The higher levels of bioerosion, micritic crusts and encrustation in bioclastic floatstones than in shell concentrations from the siliciclastic intervals indicate longer residence times and/or a higher rate of the shell alteration processes. As bioclastic floatstones are limited to the carbonate intervals, this difference in shell alteration can be due to the difference in taphonomic regimes between siliciclastic and carbonate settings (Best and Kidwell, 2000; Kidwell et al., 2005). However, the higher levels of shell alteration in bioclastic floatstones can be partly caused by higher proportion of epifaunal bivalves and brachiopods in the carbonate intervals as compared to more common infaunal and semi-infaunal bivalves in the siliciclastic intervals.

The carbonate regime with intrinsically lower sedimentation rates and lower turbidity levels was probably more suitable for higher rates of bioerosion or encrustation. As internal stratification is commonly obliterated, time-averaging may be additional bias affecting community composition (as opposed to transport, Fürsich and Aberhan, 1990; Olszewski, 2004). For the present purposes it is assumed that although bioclastic floatstones can be of multiple-event origin; they are more or less within-habitat time-averaged. As bioclastic floatstones with bivalves and brachiopods show some signs of internal stratification and stacked bioclasts, they were deposited near normal or maximum storm wave base. A high proportion of micrite, low proportions of disarticulated valves and poor sorting of floatstones indicate rather limited reworking. Bivalve packstones show signs of amalgamation, indicating substantial reworking above fair-weather wave base.

6. Estimation of effects of storm-reworking on compositional fidelity

6.1. Theoretical concept

Two simplified scenarios related to the effect of storm-reworking on community composition can be recognized (Fig. 8). Either (1) one community is affected by sorting, or (2) in addition to within-community sorting, two or more communities are mixed. If the sorting and mixing importantly bias the original community composition, distinct patterns in relationship between reworked and non-reworked assemblages should be produced in Q-mode ordination space. For simplicity of graphic presentation, assemblages in the theoretical scenarios presented below contain only two taxa so they can be plotted in a bivariate plot, with axes representing their absolute numerical abundance. Arbitrary values are deliberately chosen in order to show small and large differences between reworked and non-reworked assemblages under sorting and mixing scenarios (Appendix). When dealing with real fossil assemblages, compositional patterns of multi-species samples can be evaluated in an analogous way in NMDS. Although the explanatory bivariate plots use absolute abundances and NMDS is based on rank abundances, the basic concept of assemblage relationship is based on an equivalent principle (i.e., distance between samples should be related to sample dissimilarity).

6.1.1. Sorting of one community

In this scenario, a community can be affected by differential sorting (there is no potential for mixing as there are no other communities, Fig. 8A). In the bivariate plot, the two taxa are approximately equally abundant in five non-reworked assemblages. These five assemblages can be supposed to reflect variation in an original community composition. Taxon A is more resistant to transport and taxon B is more susceptible to transport. During reworking, one of five non-reworked assemblages is affected by sorting.

If differential sorting is effective, a residual assemblage dominated by taxon A will be present, as well as a transported assemblage dominated by taxon B. Fig. 9A shows such hypothetical situation where the composition of the reworked and non-reworked assemblages is substantially different (90% of specimens of each taxon are transported in accord with their expected hydrodynamic behavior). Therefore, if significant differences in composition occur between real reworked and non-reworked assemblages (e.g., tested with ANOSIM), fidelity is probably substantially biased in reworked assemblages. As the example of within-community sorting, the Cambrian trilobite assemblages of southern Alberta can be used. Westrop (1986) suggested that the assemblages were sorted into two continuously intergrading assemblages dominated by small- and large-sized trilobites.

Alternatively, if differential sorting of one community is ineffective, small differences in community

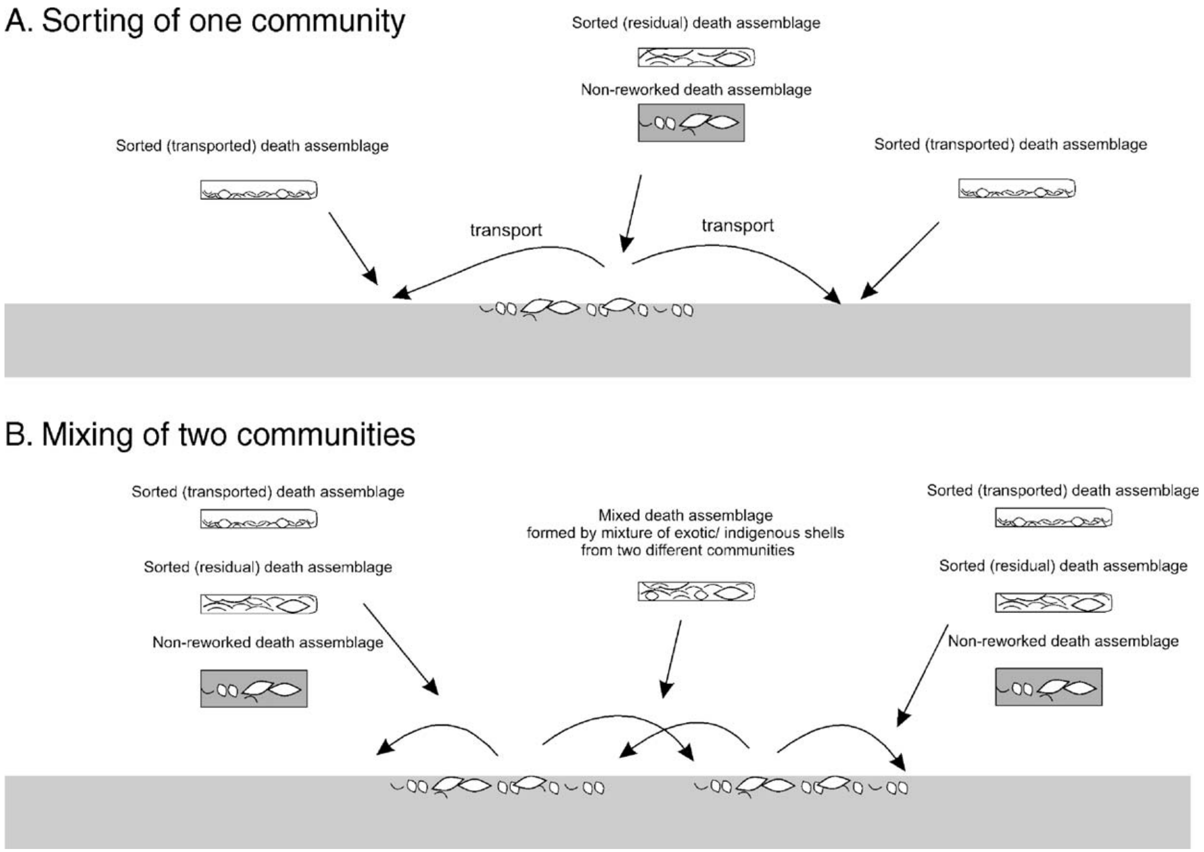


Fig. 8. Graphic representation of effects of storm-reworking that can change composition of fossil assemblages.

composition will exist in spite of sedimentologic evidence for storm-reworking. In the extreme hypothetical scenario shown in Fig. 9B, only 10% of specimens of taxon B are winnowed, or 90% of specimens of taxon A are transported together with all specimens of taxon B. This scenario leads to subtle differences in composition between non-reworked and reworked assemblages. In this case it can be argued that storm-reworking did not substantially alter the original composition, because reworked assemblages do not substantially exceed the range of compositional variation typical of non-reworked assemblages. Note that the within-community comparison of reworked and non-reworked assemblages can be used also when the two taxa differ in their resistance to post-mortem destruction (i.e., preferential destruction of less durable taxa will lead to an assemblage dominated by more durable taxa).

6.1.2. Mixing of two communities

During a mixing process, one assemblage from the first community is allowed to be mixed with one assemblage from the second community. As in the previous case, both communities can be affected by within-community sorting. In Fig. 10A, the possible range of reworked assemblages due to within-community sorting is shown by grey shaded areas. If two communities are mixed, the reworked assemblages can show compositions that cannot be produced by within-community sorting alone (Fig. 10B).

In the case of two communities shown in Fig. 10, some overlap exists between assemblages that can arise through within-community sorting and between-community mixing. This overlap occurs because the original communities differ only in the abundances of the same two taxa. However, in multivariate space formed by multi-species assemblages this overlap should be smaller. Theoretically, the overlap between mixed and sorted assemblages will be lower with increasing dissimilarity between the two original communities. In summary, the prediction for mixing scenario will be that substantially mixed assemblages should be preferentially present in intermediate position between non-reworked assemblages of two original communities, and should exceed the range of within-community variation defined by non-

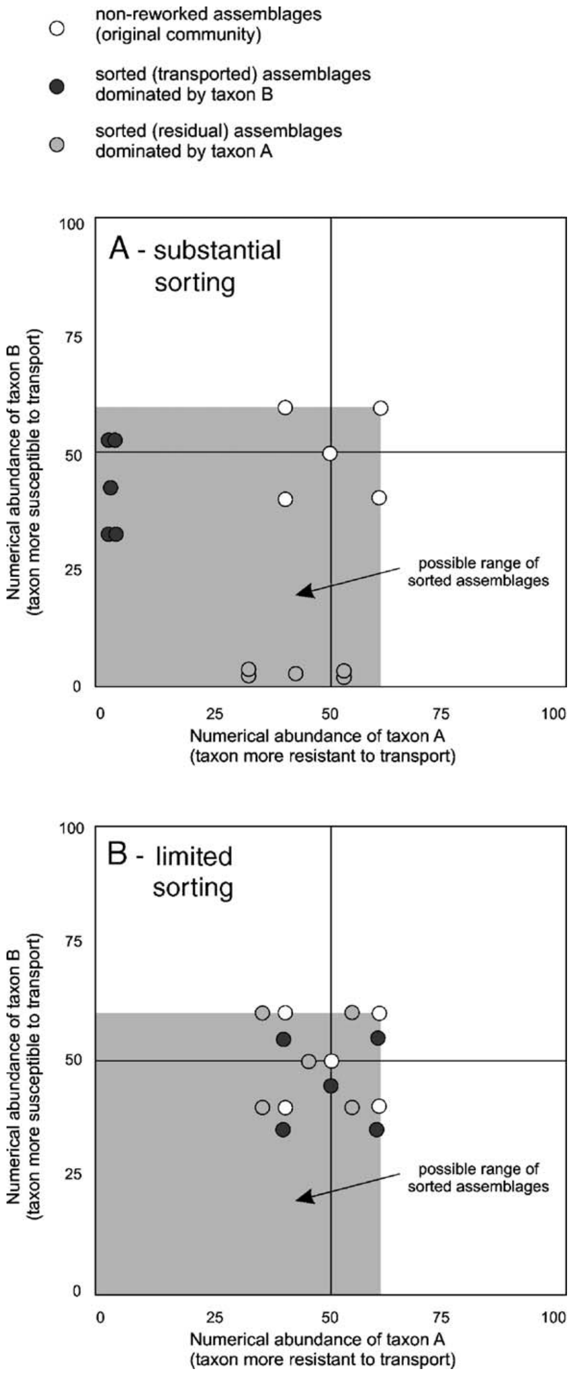


Fig. 9. Two simplified scenarios for one community affected by sorting: (A) The composition of both reworked assemblages is substantially different from non-reworked assemblages. (B) The composition of reworked assemblages is not different from non-reworked assemblages (i.e., it does not exceed within-community variation defined by non-reworked samples).

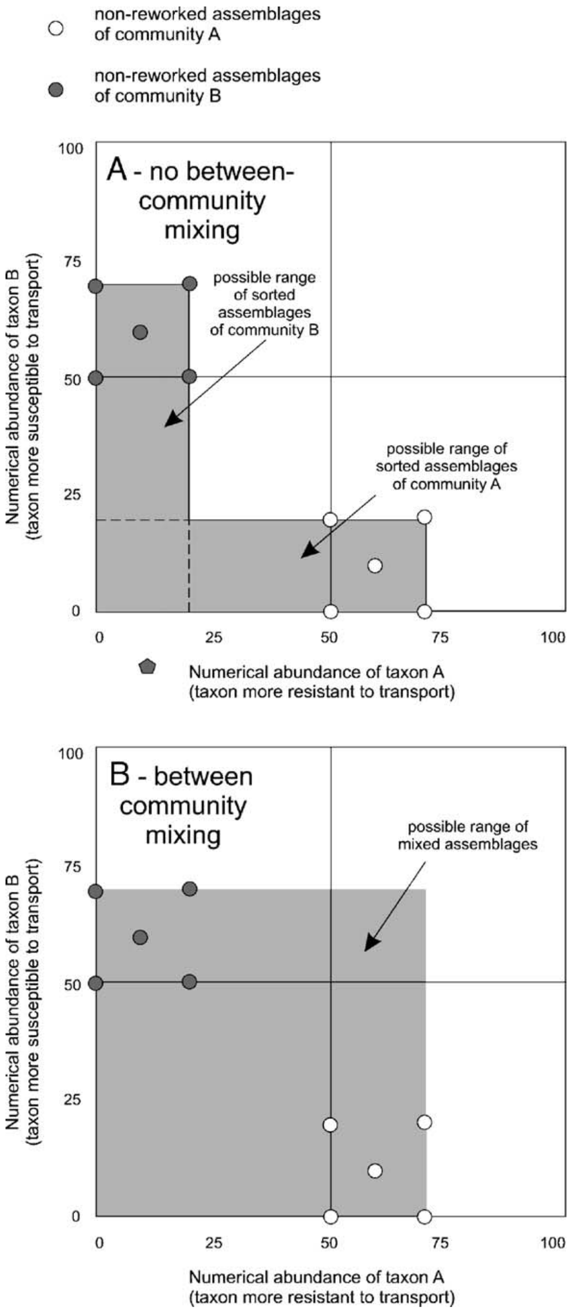


Fig. 10. Two simplified scenarios for between-community mixing. (A) Two grey shaded areas show a possible range of sorted assemblages that can arise from one or another community. In a scenario without between-community mixing, no reworked assemblages will be present with the composition intermediary between the two distinct communities. (B) Grey shaded area shows a possible range of mixed assemblages. Although there is some overlap with sorted assemblages from Fig. 10A, substantially mixed assemblages can show an intermediate composition that cannot be produced by within-community sorting alone.

Table 3
Summary of the three datasets used in this study

Shell concentration type	Exhaustive dataset	1st restrictive dataset	2nd restrictive dataset
Packstones	x		
Pavements with large bivalves	x		
Floatstones with large bivalves	x	x	
Bioclastic marlstones	x	x	x
Bioclastic floatstones	x	x	x
Sample group	Number of samples	Number of samples	Number of samples
Isocyprina	7	0	0
Bakevellia	2	0	0
Myophoriopis	15	7	7
Gervillaria	11	7	1
Cassianella	2	2	2
Chlamys	2	2	2
Rhaetina gregaria	10	7	7
Rhaetina pyriformis	4	4	4

In addition to bioclastic floatstones and bioclastic marlstones, the first restrictive dataset includes also floatstones with large bivalves which show some effects of reworking, but rather in situ without substantial transport. The second restrictive dataset is more conservative and includes bioclastic marlstones and bioclastic floatstones only. Although some samples belonging to bioclastic floatstones show signs of reworking, assemblages with quantitative data used specifically in this study are affected by minimum reworking.

reworked assemblages. If one of the original communities will not be preserved in the fossil record, mixed assemblages can show consistent compositional difference in comparison to non-reworked assemblages of the second community (similarly as in the scenario with effective differential sorting).

6.2. Results

Based on the genetic interpretation of shell concentrations, individual assemblages were assigned to reworked and non-reworked types. Below, the subdivision of reworked and non-reworked assemblages follows the first restrictive dataset (Table 3). One sample group, discriminated by the cluster analysis, can theoretically contain assemblages that (1) reflect the original composition of one community, (2) belong to the differentially sorted relict of one community, or (3) represent the mixture of two or more communities. The differences between reworked and non-reworked assemblages are explored (a) within and (b) between sample groups. In addition, multivariate biotic patterns

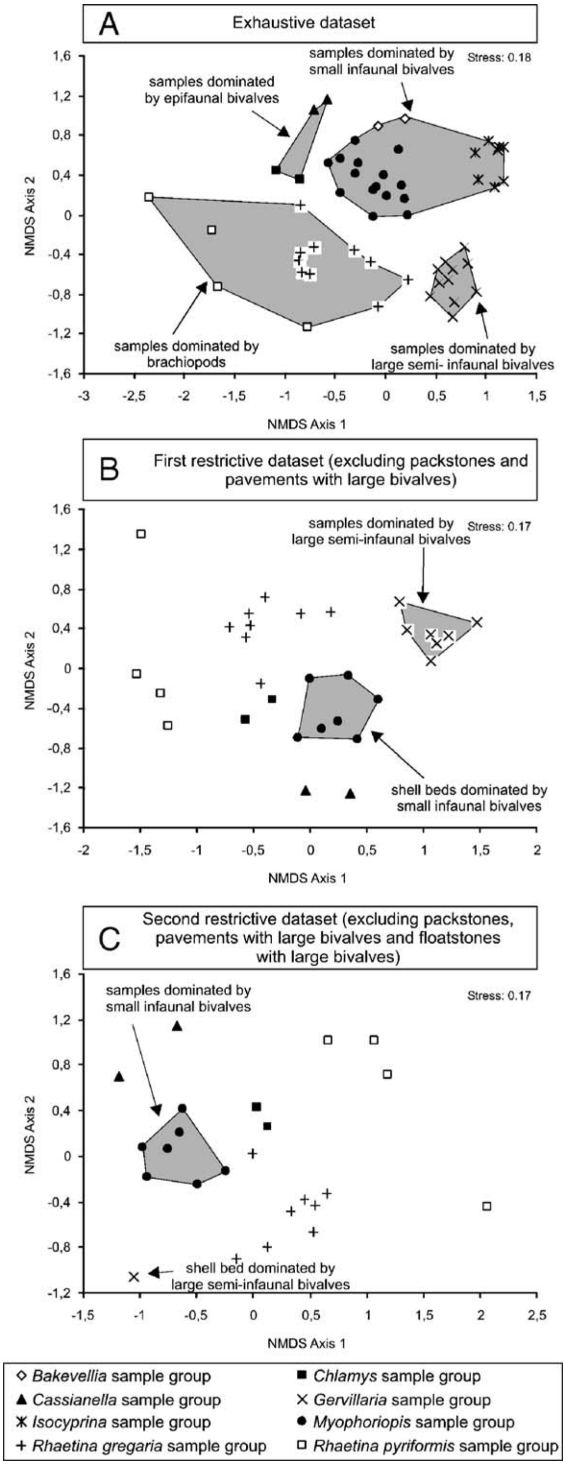


Fig. 11. (A) NMDS ordination of the exhaustive dataset with eight discriminated sample groups. (B) NMDS of the first restrictive dataset (excluding packstones and pavements with large bivalves). Note that the segregation between small and large-bivalve dominated sample groups persists. (C) NMDS of the second restrictive dataset (excluding packstones, floatstones with large bivalves and pavements with large bivalves). Six of eight sample groups persist even after the most severe data reduction.

based on all assemblages and non-reworked assemblages are compared in the exhaustive and restrictive datasets.

As follows from the theoretical scenarios, if there is substantial within-community differential sorting or between-community mixing, reworked assemblages can show either different compositions compared to non-reworked assemblages or they can occupy intermediate position between non-reworked assemblages of distinct sample groups.

6.2.1. Comparison of exhaustive and restrictive datasets

In order to evaluate how an exclusion of reworked assemblages from multivariate analysis affects its results, the compositional pattern based on reworked and non-reworked assemblages (exhaustive dataset) is compared with the pattern based on non-reworked assemblages only (two restrictive datasets, Table 3). In NMDS of the exhaustive dataset, eight sample groups discriminated by the cluster analysis are mostly well segregated (Fig. 11A). There is no one-to-one correspondence between shell concentration types and sample groups. On one hand, some sample groups occur in several shell concentration types. On the other hand, one shell concentration type can contain more sample groups. The *Isocyprina* and *Bakevellia* sample groups are preserved only in packstones.

In the first restrictive dataset including floatstones with large bivalves (Fig. 11B), two sample groups dominated by small bivalves are missing (*Isocyprina* and *Bakevellia*) (Table 3). The sample groups dominated by small (*Myophoriopis*) and large (*Gervillaria*) bivalves are still distinctly separated in NMDS. There is thus persistence of small and large bivalve-dominated sample groups even after the exclusion of reworked assemblages. Excluding further floatstones with large bivalves (the second restrictive dataset, Table 3), only one assemblage represents the *Gervillaria* sample group in NMDS (Fig. 11C). However, six sample groups can still be distinguished even after the most severe data reduction.

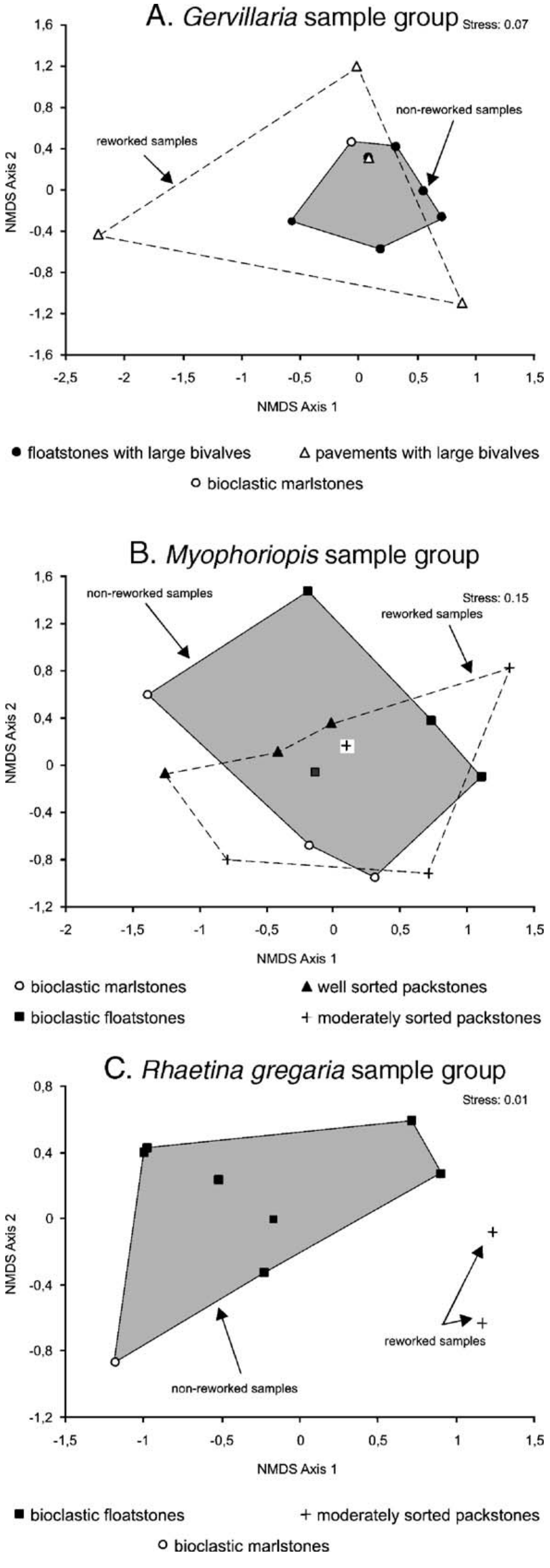


Fig. 12. Within-sample group comparisons of reworked and non-reworked assemblages. (A) NMDS of the *Gervillaria* sample group. Although some reworked assemblages exceed the variation defined by non-reworked assemblages, reworked and non-reworked assemblages show similar composition. (B) NMDS of the *Myophoriopis* sample group. Reworked and non-reworked assemblages overlap to a large degree. (C) NMDS of the *Rhaetina gregaria* sample group. Reworked assemblages show different composition in contrast to non-reworked assemblages.

6.2.2. Within-sample group biotic comparisons

Differences in composition between the reworked and non-reworked assemblages are analyzed in three sample groups. NMDS of the *Myophoriopis* sample group indicates no consistent relationship between taxonomic composition and shell concentration type (Fig. 12). The compositional difference between reworked and non-reworked assemblages is insignificant ($R = 0.02$; $p = 0.35$). The composition of the reworked assemblages mostly falls within the range of the within-community variation defined by non-reworked assemblages. Similarly, the *Gervillaria* sample group occurs in several shell concentration types, including marlstones, floatstones with large bivalves and pavements with large bivalves (Fig. 12). Within-community variation defined by non-reworked assemblages is slightly exceeded by reworked assemblages in this sample group. ANOSIM testing between non-reworked and reworked assemblages ($R = 0.092$; $p = 0.27$, Table 4) shows no significant differences. Although defining the level of significance for the *R. gregaria* sample group is limited (36 possible permutations cause that the p-value cannot be lower than 0.028), a relatively high R statistic ($R = 0.56$) and NMDS indicate some differences between two reworked and seven non-reworked assemblages (Fig. 12, Table 4).

6.2.3. Between-sample group biotic comparisons

In order to minimize heterogeneity in composition due to differences among stratigraphic units, compositional patterns are separately evaluated in Unit 2 and in units 3–4. There is a large segregation between three sample groups in Unit 2 (Fig. 13A). Reworked assemblages are mostly not in intermediate position between non-reworked assemblages of distinct sample groups. Only one reworked assemblage (K1) lies in intermediate position between the *Gervillaria* and *R. gregaria* sample groups.

Similarly, the sample groups in Unit 3 are well segregated and do not show any overlap (Fig. 13B). Focusing on the *Myophoriopis* and *Gervillaria* sample groups with high number of samples, the space between non-reworked assemblages of the two sample groups is not preferentially occupied by reworked assemblages. As the position of assemblages in NMDS ordination depends also on other sample groups and the stress value is relatively high (0.14), only the *Gervillaria* and *Myophoriopis* sample groups were plotted to minimize this variation (Fig. 13C). The same pattern follows, with segregation of two sample groups. Reworked assemblages of the *Myophoriopis* sample group are not more similar in composition to assemblages of the *Gervillaria* sample group than non-reworked assemblages of the *Myophoriopis* sample group.

6.2.4. Size–frequency distributions

In the *Isocyprina* sample group, SFDs of *Isocyprina alpina* are unimodal and bell-shaped, with mode at 4 or 5 mm (Fig. 14). However, SFDs of other species (*Bakevellia praecursor* or *Nuculana claviformis*) from the same assemblages show multimodal patterns and their modes are in different size classes than those of *Isocyprina alpina* (e.g., *Bakevellia praecursor* has the mode between 6 and 9 mm). The Kolmogorov–Smirnov and Wilcoxon rank sum tests show significant between-species differences for all four assemblages (Table 5). In order to estimate the effects of sorting on diversity of Miocene assemblages, Zuschin et al. (2004) tested if within-sample SFDs are significantly more similar to each other than between-sample SFDs. However, most of samples in this study are paucispecific and do not contain more than two species with sufficient number of individuals, so this test is not used here. In floatstones with large bivalves, *Gervillaria inflata* has either a multimodal or unimodal, and right- or left-skewed SFDs (Fig. 15). In pavements with large bivalves, *Gervillaria inflata* has right-skewed SFD dominated by smaller specimens (Fig. 15).

6.2.5. Right–left valve ratios

In floatstones with large bivalves, three assemblages show significantly lower proportions of *Gervillaria* right valves; two assemblages show more or less the expected proportions (Fig. 16). In packstones, *Bakevellia* shows mostly significantly lower proportions of

Table 4
Results of ANOSIM for the *Myophoriopis*, *Gervillaria* and *Rhaetina gregaria* sample groups

Comparison of reworked vs. non-reworked assemblages	Observed R	p-value	Permutations	Number of permuted $R \geq$ observed R
Myophoriopis sample group	0.02	0.35	6435	2253
Gervillaria sample group	0.216	0.109	330	36
Rhaetina gregaria sample group	0.558	0.028	36	1

The Bonferroni correction lowers the alpha value to 0.016.

right valves from the expected proportion of 50 : 50 (Fig. 16). *Isocyprina* and *Myophoriopis* show variable proportions but mostly not significantly different from the expected proportion (Fig. 16). In bioclastic marlstones and bioclastic floatstones, *Myophoriopis* shows the expected proportions, although in one assemblage there is under-representation of right valves. *Rhaetina gregaria* shows significantly lower proportions of dorsal valves in bioclastic floatstones (Fig. 16).

6.3. Discussion

Three arguments indicate that storm-reworking did not substantially affect compositional fidelity and did not lead to sorted or mixed assemblages with substantially biased compositions. The reworked shell concentrations probably reflect the primary composition of original community being affected by the storm. These arguments are supplemented by size patterns and valve ratios.

(1) Six of eight sample groups delimited on the basis of the exhaustive dataset persist in the first and the second restrictive dataset. In particular, the segregation of sample groups dominated by small and large bivalves remains when reworked assemblages are excluded. Therefore, their presence in non-reworked assemblages shows that this compositional difference is not the artifact of sorting or mixing.

(2) In the *Myophoriopis* and *Gervillaria* sample groups, reworked and non-reworked assemblages are very similar in composition and mostly do not show consistent differences that would be expected if differential sorting or mixing had occurred (e.g., reworked assemblages do not substantially exceed the range of variation defined by non-reworked assemblages). In the *R. gregaria* sample group there is probably some effect of transport and reworked assemblages can be substantially biased in composition.

(3) Based on between-sample group comparisons, reworked assemblages do not preferentially occupy an intermediate position between non-reworked assemblages of particular sample groups, indicating that reworking mostly did not lead to artifactual assemblages. Only the position of reworked

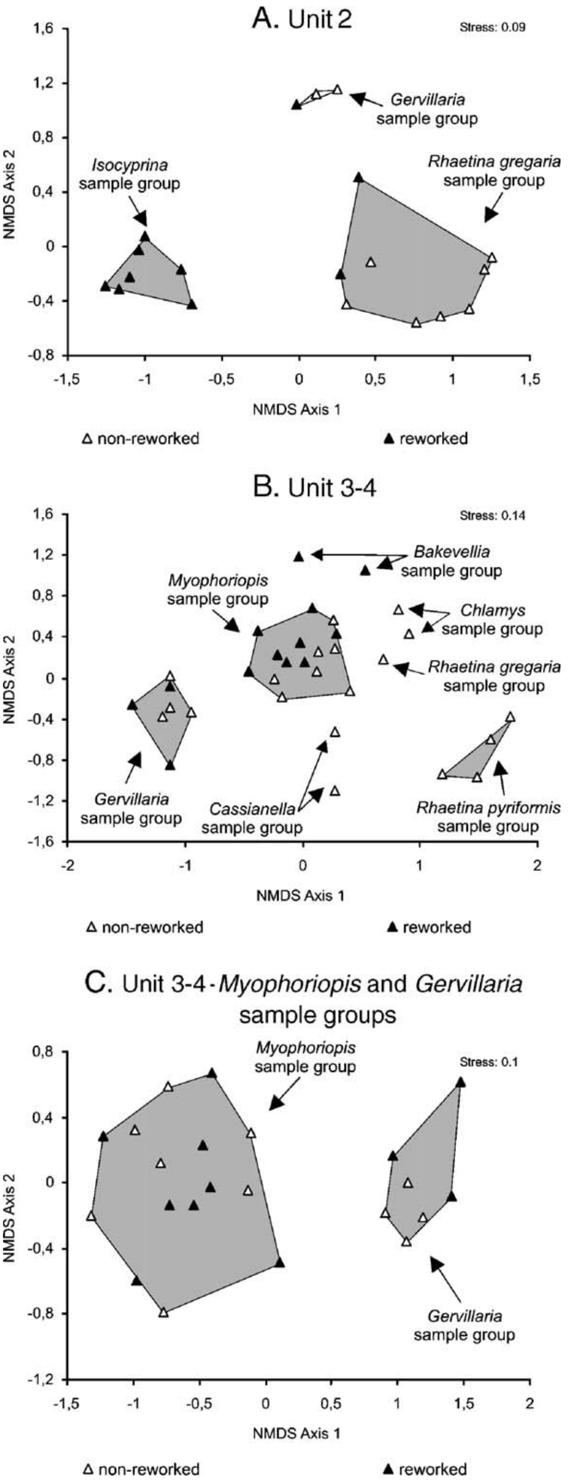


Fig. 13. Between-sample group comparisons of reworked and non-reworked assemblages. (A) NMDS of Unit 2. With the exception of assemblage K1, reworked assemblages do not preferentially occupy positions between sample groups. This pattern indicates rather limited between-community mixing. (B) NMDS of Units 3 and 4. Note the segregation between the *Myophoriopis* and *Gervillaria* sample groups, without intermediate reworked assemblages. (C) NMDS of the *Gervillaria* and *Myophoriopis* sample groups. Other sample groups were excluded to lower the stress value.

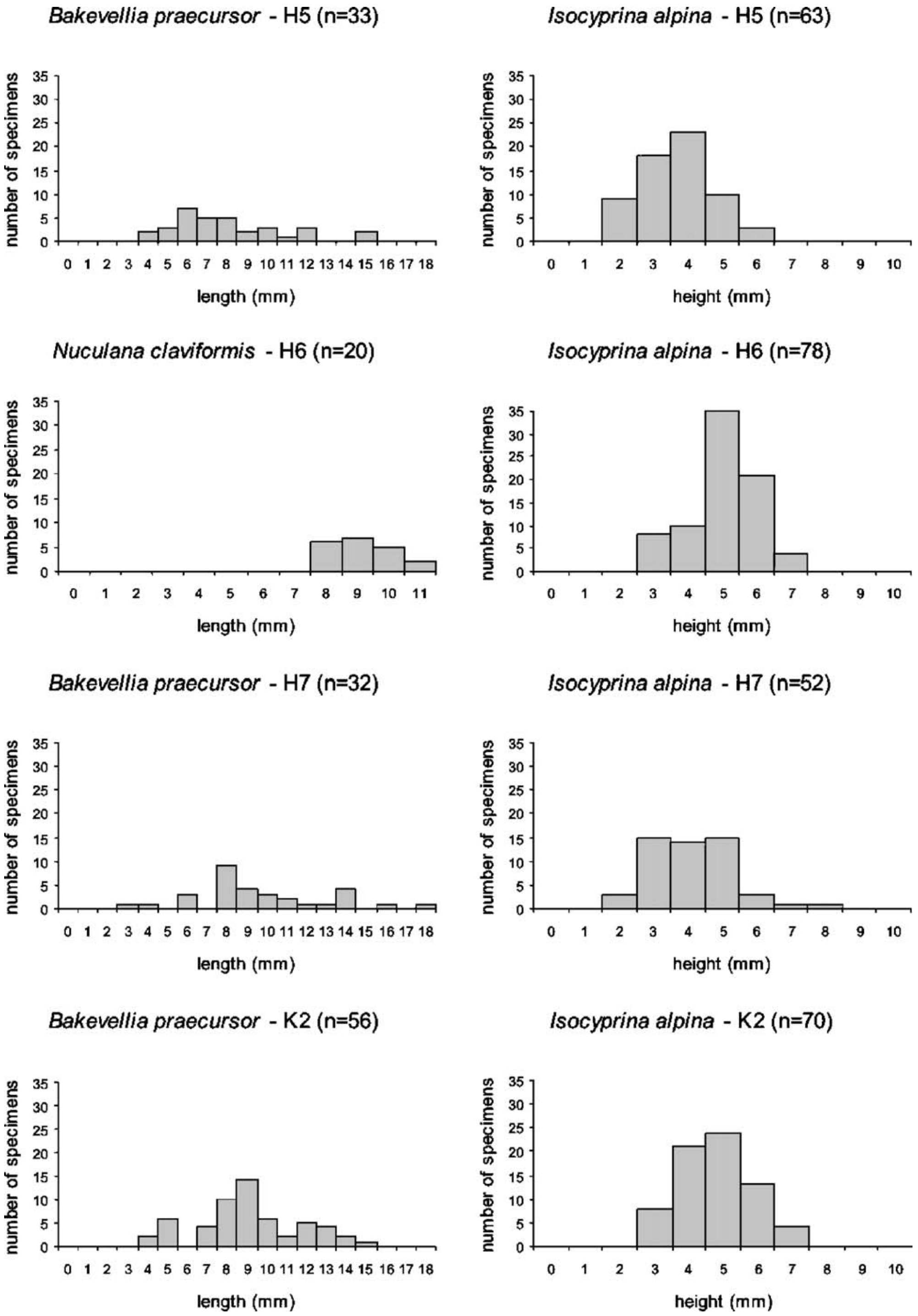


Fig. 14. Size–frequency distributions of *Isocyprina* and co-occurring small bivalves in packstones. Species co-occurring in one assemblage show different size modes. The Kolmogorov–Smirnov and Wilcoxon tests show significant differences in four pairwise comparisons.

assemblage K1 can be in accord with the predicted pattern of mixing between the *Gervillaria* and *R. gregaria* sample groups. Two sample groups represented only by reworked assemblages (*Isocyprina* and *Bakevellia* sample groups) can be theoretically produced by sorting or mixing, but their non-reworked counterparts are not preserved. However, due to their distinct composition

Table 5
Results of non-parametric K–S and Wilcoxon tests for pairwise comparisons in four samples of *Isocyprina* sample group

Sample	Pairwise comparisons	Kolmogorov–Smirnov test	Wilcoxon test
H5	*Isocyprina alpina* vs. *Bakevellia praecursor*	D = 0.86; $p < 0.00001$	$Z = 5.01$; $p < 0.00001$
H6	*Isocyprina alpina* vs. *Nuculana claviformis*	D = 1; $p < 0.00001$	$Z = 3.91$; $p = 0.00008$
H7	*Isocyprina alpina* vs. *Bakevellia praecursor*	D = 0.89; $p < 0.00001$	$Z = 4.88$; $p < 0.00001$
K2	*Isocyprina alpina* vs. *Bakevellia praecursor*	D = 0.81; $p < 0.00001$	$Z = 6.38$; $p < 0.00001$

The Bonferroni correction lowers the alpha value to 0.0125.

and SFDs it is improbable that they are sorted relicts of the six remaining sample groups.

(4) Body size patterns support previous interpretations of limited within-community sorting. SFDs are especially helpful in evaluation of those sample groups that are represented only by reworked assemblages. Multimodal SFDs of *Bakevellia praecursor* and *Nuculana claviformis* in the *Isocyprina* sample group, and significant within-sample differences indicate that although dominated by small species, hydrodynamic sorting did not generate this size pattern (Fig. 14). It thus seems that although the *Isocyprina* sample group is preserved in packstones only, it still represents a relict of an original community, rather than an artifact of mixing or sorting. The size range of *Nuculana* and *Bakevellia* in packstones overlaps with smaller, 10–15 mm long *Gervillaria* valves (this size class is commonly present in floatstones or pavements with large bivalves). If the *Isocyprina* sample group would represent a sorted relict, it should also contain smaller *Ger-*

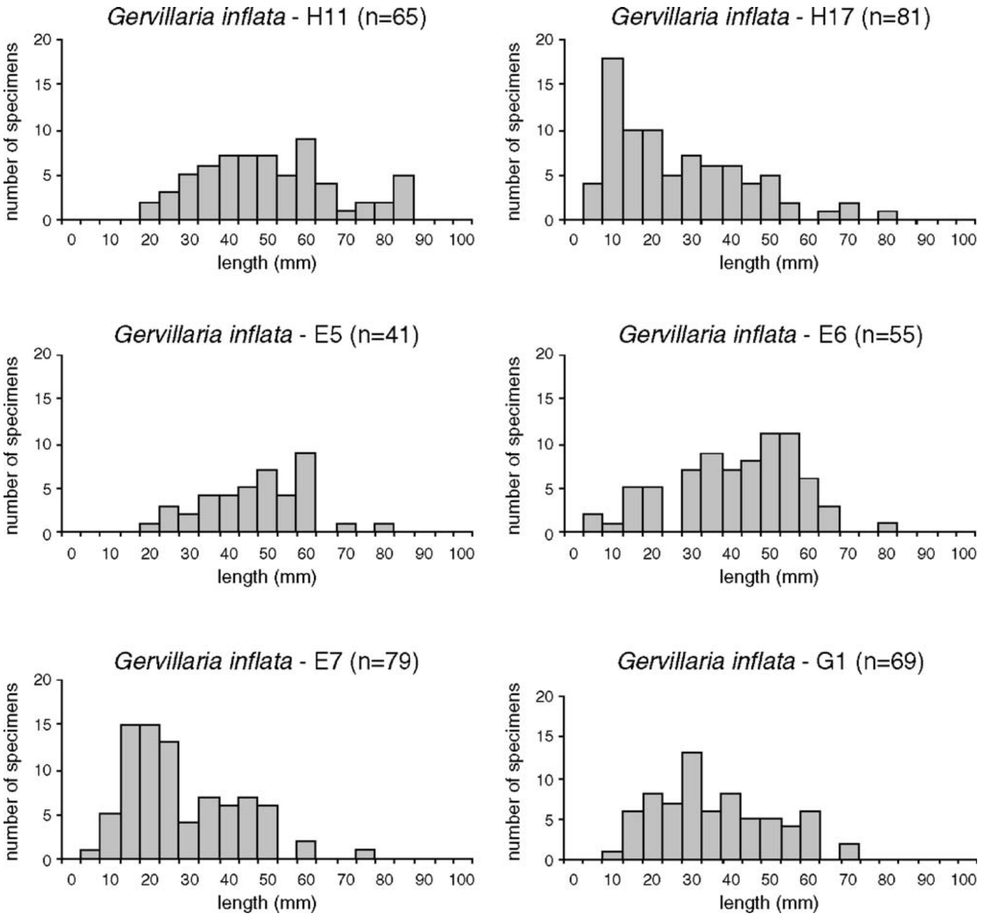


Fig. 15. Size–frequency distributions of *Gervillaria* in floatstones with large bivalves (Samples H11, E5, E6, E7 and G1) and pavements with large bivalves (Sample H17).

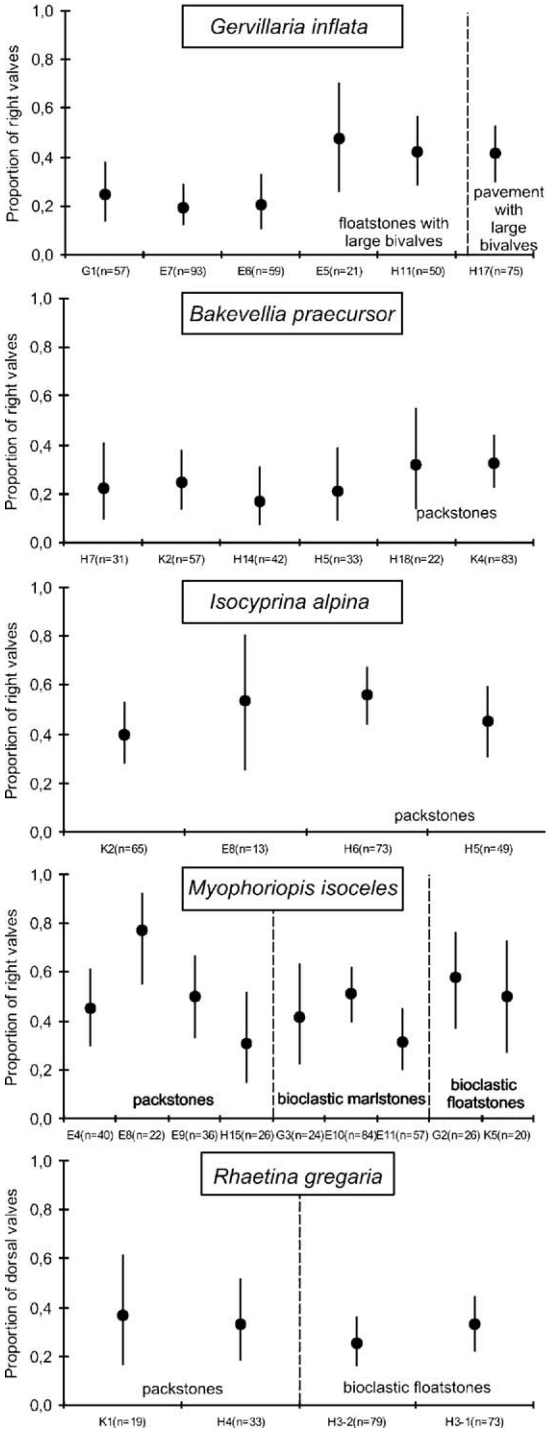


Fig. 16. Proportions of right valves in four bivalve species and proportions of dorsal valve in brachiopod *R. gregaria*. 95% confidence intervals were calculated with binomial equation (Zar, 1996).

villaria valves. Also, winnowing is not responsible for absence of small bivalves from pavements/floatstones with large bivalves, because small *Gervillaria* specimens are of comparable sizes as small bivalves in the *Isocyprina* or *Myophoriopis* sample groups.

(5) Right–left valve ratios significantly different from the expected 50 : 50 are commonly used as evidence for compositional bias due to under-representation of one valve (Kornicker et al., 1963; Behrens and Watson, 1969; Frey and Henderson, 1987; Powell et al., 1989; Simões and Kowalewski, 1998; Shimoyama and Fujisaka, 1992; Zuschin and Stanton, 2002). That there is some compositional bias is indicated by under-representation of right valves in inequivalve bakevellid bivalves (i.e., *Gervillaria* in floatstones with large bivalves and *Bakevellia* in packstones). The left valve of *Gervillaria* is of different shape and substantially more convex than the right valve. The shell is less inequivalve in *Bakevellia*. These between-valve differences can lead to differential susceptibility to destruction or transport. In brachiopods, it is known that less convex dorsal valves are less robust and more prone to destruction than the ventral valves (Holland, 1988; Velbel and Brandt, 1989, Alexander, 1990; Daley, 1993). This differential preservation holds for *Rhaetina gregaria* with under-represented dorsal, less convex valves. Note that the relative abundances used in the multivariate analyses are based on the approach that eliminates the problem with differential preservation of one or another valve (i.e., only the more common valve type is counted). Therefore, although some species in the reworked assemblages are affected by the compositional bias with respect to right–left valve ratios, sample-level relative abundances and multivariate analyses are not affected by this bias.

7. Distribution of shell concentrations along onshore–offshore gradient

7.1. Stratigraphic distribution of shell concentrations

In Unit 2, a typical feature is that mm-scale planar and wavy laminations may start near the base of the siliciclastic intervals (Fig. 3). In contrast, hummocky-cross stratification (HCS) is typically present in the middle and upper parts of the siliciclastic intervals in Unit 2. Packstones and bioclastic marlstones are mostly present in the lower parts and pavements and floatstones with large bivalves in the middle parts and upper of the siliciclastic intervals. In Unit 2, shell bed frequency is generally higher in the lower and middle parts of the siliciclastic intervals in contrast to the upper parts (Fig. 3). The carbonate intervals in Unit 2 consist of coral-debris floatstones and bioclastic floatstones with bivalves and brachiopods. In the lower parts of Unit 3 (Fig. 4), the siliciclastic intervals are characterized by a relatively thick marl interval at the base, followed by mm-scale planar/wavy-stratified limestone beds with packstones in the middle parts and floatstones and pavements with large bivalves in the upper parts of the siliciclastic intervals. HCS in Unit 3 is less common than in Unit 2. The stratigraphic distribution of shell concentrations in the siliciclastic intervals thus differs between Unit 2 and 3. The carbonate intervals in lower parts of Unit 3 are mainly represented by bioclastic floatstones. The discriminated sample groups show a regular replacement pattern within the siliciclastic intervals in Unit 2 and the lower parts of Unit 3. Sample groups dominated by brachiopods can be present just near the base of the siliciclastic intervals. In the lower parts of the siliciclastic intervals, sample groups dominated by small bivalves mainly occur. Sample groups dominated by large bivalves are typical of the middle and upper parts of the siliciclastic intervals.

As follows from the stratigraphic replacement of marls by planar/wavy-stratified beds and HCS, the siliciclastic intervals reflect a shallowing-upward trend recording an increase in storm frequency and intensity. Due to the gradual deepening trend within the Hochalm Member, shell concentrations that are common in the upper parts of the siliciclastic intervals in Unit 3 do not reflect the shallowest habitats as do the upper parts of the siliciclastic intervals in Unit 2. Shell concentrations of Unit 3 thus represent a deeper part of the onshore–offshore gradient than shell concentrations in Unit 2. Below, distribution of shell concentrations along the onshore–offshore gradient in the Kössen Basin is thus interpreted for the siliciclastic intervals in Unit 2 and the lower parts of Unit 3. Although the carbonate intervals were supposed to represent the shallowest part of the small-scale sequences by Golebiowski (1991), they are not treated here because their sedimentologic features do not invariably indicate shallower conditions. Shell concentrations from the upper parts of Unit 3 and Unit 4 reflect only habitats below normal or maximum storm wave base and their onshore–offshore distribution is thus not interpreted.

7.2. Variations in hardpart-input rates along onshore–offshore gradient

Shell concentrations are widely used for interpretation of onshore–offshore gradients because storm intensity and frequency generally negatively correlate with increasing depth/distance from shore (Aigner, 1979, 1982, 1985; Norris, 1996; Myrow and Southard, 1996; Nebelsick and Kroh, 2002). This correlation leads to the predictable distribution of shell concentration in an onshore–offshore gradient, with thick, amalgamated shell concentrations in the proximal position and thin, graded and well sorted shell concentrations in the distal position. Deviations from this simple trend were discussed by Fürsich and Oschmann (1986). As they pointed out, the thickness of shell concentration depends not only on the erosional storm capacity, but also on the amount of hardparts available. This hardpart amount depends on dead-shell production rates and background shell destruction rates.

In the light of the interpreted genesis of shell concentrations, their compositional fidelity and stratigraphic distribution within the siliciclastic intervals, primary variations in hardpart-input rates had probably strong influence on the distribution of shell concentrations along the onshore–offshore gradient in the Kössen Basin. Three factors lead to atypical features in the onshore–offshore distribution of shell concentrations of the Kössen Formation (Fig. 17). First, high background shell destruction rates probably inhibited any formation of thick, amalgamated shell concentrations. Second, either a decrease in dead-shell production rates and/or an increase in shell destruction rates were associated with the shallowing-upward trend that is recorded by the siliciclastic intervals in Unit 2. This decrease in hardpart-input rates led to less common shell concentrations in shallow than in deep habitats. Third, between-habitat differences in body size pattern caused differences in fabric of shell concentrations.

(1) Many tempestites with planar/wavy lamination or HCS in the siliciclastic intervals are shell-poor. As single-event shell concentrations are embedded between marlstones without any shells, it is difficult to assume that the high shell density in event beds is only due to winnowing or concentration of shells from shell-poor marls. Shell destruction rates were probably high during deposition of marls, possibly due to dissolution via organic decomposition and sulphate reduction. They could thus cause low potential for passive accumulation of dead shells during background conditions, limiting potential for formation of thick shell concentrations. On one hand, shell-rich tempestites thus contain only shells which were alive at the time of the storm event or which represent recently dead individuals. On the other hand, shell-poor tempes-

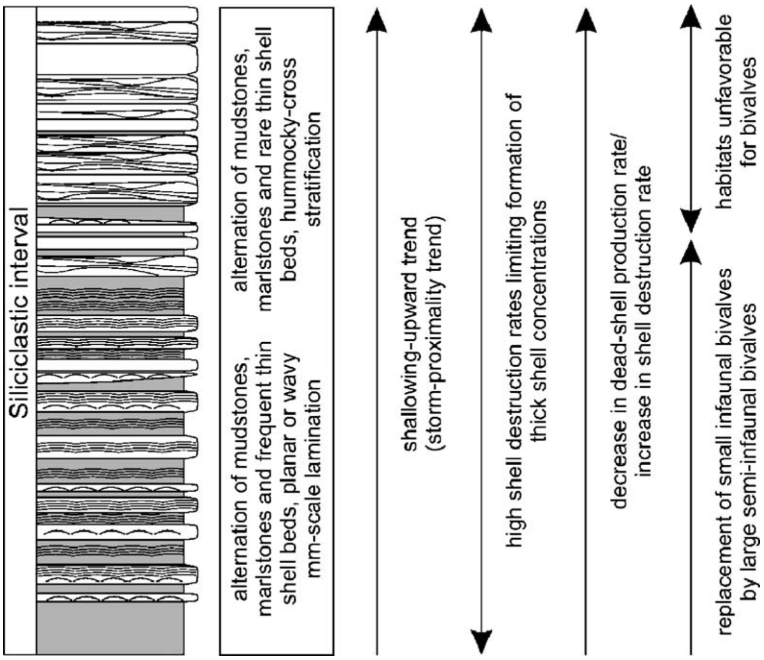
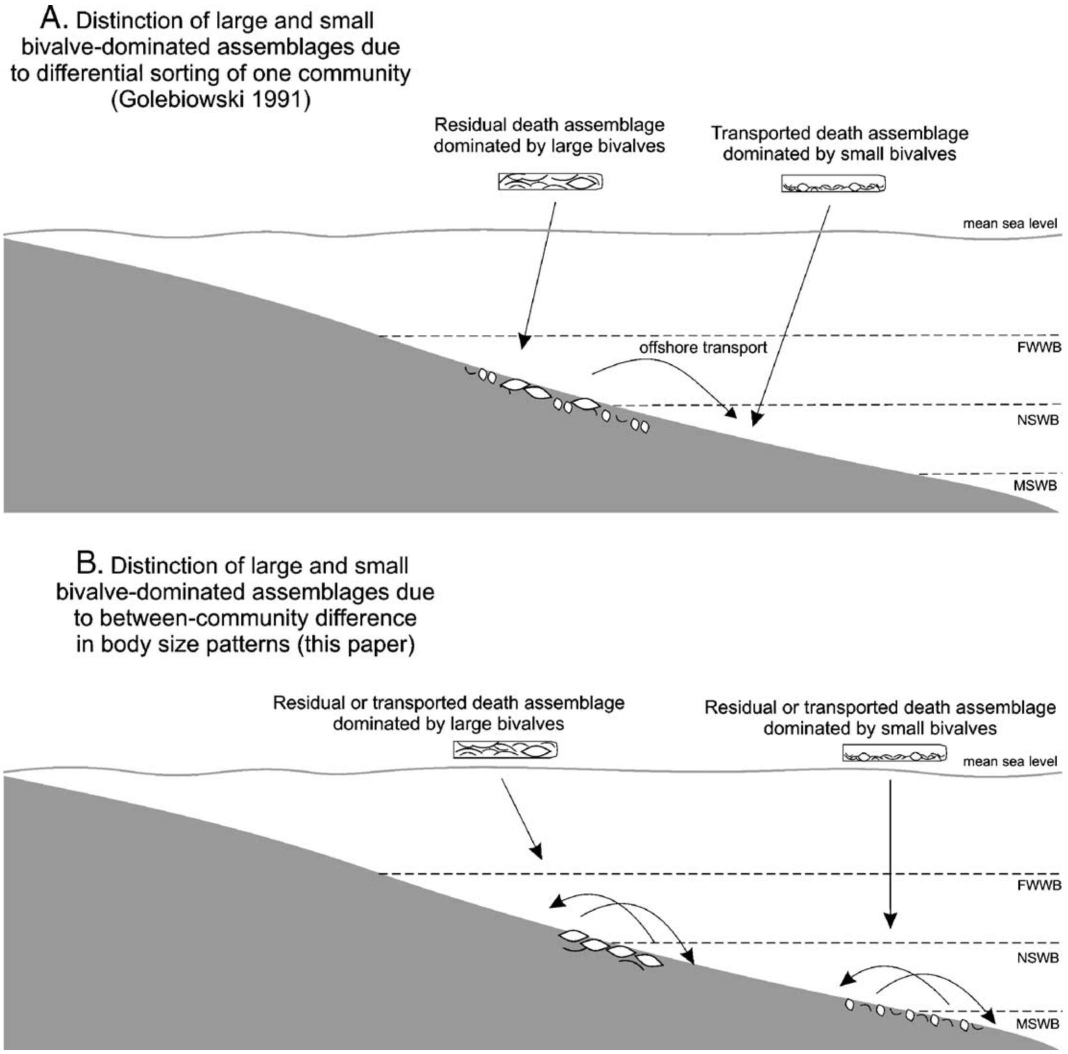


Fig. 17. Simplified stratigraphic distribution of shell concentrations in the siliciclastic intervals of Unit 2. Co-variations of hardpart-input rate with the shallowing-upward trend specifically influence frequency and biofabric of shell concentrations.

tites would imply that the sea-floor affected by the storm event contained almost no live or recently dead bivalve shells.

(2) Shell-poor tempestites are especially common in the upper parts of the siliciclastic intervals in Unit 2, in contrast to more common shell-rich tempestites in their lower parts. However, the upper parts of the siliciclastic intervals in Unit 2 show sedimentologic evidence for higher storm intensity/ frequency. Therefore, the higher frequency of shell concentrations in the lower parts of the siliciclastic intervals in Unit 2 is in contrast to the expectation that shelliness and shell concentration frequency should increase towards shallower habitats (up to the point where amalgamation starts to prevail). The distribution of shell concentrations along the onshore–offshore gradient of the Kössen Basin is thus reversed—shell concentrations are more common in deeper than in shallower habitats. Note that this reversal is not due to amalgamation or cannibalism of shell beds in the shallow habitats (which would lead to lower frequency in shell beds, see Aigner, 1985), indicating that an increase in storm intensity/frequency was associated either with a decrease in dead-shell production rates and/or with an increase in shell destruction rates. Low dead-shell production rates may be due to very low bivalve abundances caused by unfavorable ecologic conditions in the shallowest habitats (e.g., high storm disturbance, high sedimentation rates or high turbidity levels).

(3) Golebiowski (1991) assumed that the packstones with small bivalves are a winnowed, easily transported portion of the original community, in contrast to pavements and floatstones with large bivalves (Fig. 18A). This idea implies that these two shell concentrations are distinctly arranged along the environmental gradient because of storm-reworking. However, as was argued above, shell concentrations with large and small bivalves represent rather different benthic communities (Fig. 18B). The vertical distribution pattern of these two groups indicates that communities dominated by small bivalves occupied relatively deeper habitats relative to communities dominated by large bivalves. Indeed, this depth-related pattern means that original biotic composition mimics sorting patterns because the same body size pattern would be expected also by a sorting scenario. The differences in life habits between infaunal and semi-infaunal bivalves can indicate differences in substrate stability/consistency and thus can lead to distinct depth preferences (e.g., the decrease in substrate stability can correlate with the increase in storm intensity/frequency). For example, Kondo



A. Distinction of large and small bivalve-dominated assemblages due to differential sorting of one community (Golebiowski 1991)

B. Distinction of large and small bivalve-dominated assemblages due to between-community difference in body size patterns (this paper)

Fig. 18. Differential body size patterns along bathymetric gradient in storm-dominated environment. (A) Hypothesis predicting differential sorting of one community into two different assemblages. This hypothesis was used by Golebiowski (1991) to explain shell concentrations from siliciclastic intervals of the Hochalm Member. (B) Hypothesis predicting differential body size patterns because of original between-habitat differences. This hypothesis is proposed for shell concentrations from siliciclastic intervals of the Hochalm Member in this paper. FWWB—fair-weather wave base. NSWB—normal storm wave base. MSWB—maximum storm wave base.

(1998) showed that different burrowing abilities of soft-bottom, suspension-feeding bivalves can reflect adaptations to habitats with different intensity of reworking and rapid burial.

7.3. Onshore–offshore gradient in the siliciclastic intervals of the Hochalm Member

The resulting onshore–offshore gradient typical of the siliciclastic intervals of the Hochalm Member of the Kössen Formation can thus be reconstructed as a shift from the deepest habitats below the maximum storm wave base with rare storm disturbance up to shallow habitats above the normal storm wave base with frequent storm disturbance. Habitats with lower storm intensity/frequency around the maximum storm wave base were occupied by bivalves or rarely brachiopod communities that had some potential to be preserved as shell concentrations. The gradient can be subdivided into three habitats.

(1) Habitats around or below maximum storm wave base, influenced by distal storm flow deposition or winnowing, were dominated by small infaunal bivalves. The preferential occurrence of the *R. gregaria* sample group stratigraphically below

the communities dominated by small bivalves may indicate that deeper or more distal habitats were occupied by brachiopods. Shell concentrations are represented by autochthonous bioclastic marlstones and single-event packstones.

(2) Habitats below normal storm wave base and above maximum storm wave base with storm flow-induced deposition were inhabited by semi-infaunal bivalves. Shell concentrations influenced by storm-flow or storm-waves are represented by pavements and floatstones with large bivalves.

(3) Habitats in the upper parts of the zone affected by storm waves but still below fair-weather wave base were characterized by deposition of hummocky cross-stratified storm beds. In this habitat, the combination of low dead-shell production rated and high background destruction rates resulted mainly in shell-poor tempestites.

8. Conclusions

(1) An evaluation of compositional differences between fossil assemblages with distinct taphonomic preservation can be used to address the question of compositional fidelity in the fossil record. Although the exploration of relationship between reworked and non-reworked assemblages in NMDS is of different nature compared with actualistic live/dead studies, this method enables quantitative assessment of hypotheses about differential compositional bias in the fossil record.

(2) The composition of shell concentrations in the Upper Triassic Kössen Formation is not substantially affected by sorting or mixing, in spite of sedimentologic evidence of storm-reworking. First, most of the sample groups based on the exhaustive dataset persist when only non-reworked assemblages are analyzed. Second, reworked and non-reworked assemblages belonging to one sample group are mostly highly similar. Third, reworked assemblages mostly do not show intermediate composition when compared to non-reworked assemblages of distinct sample groups. In addition, size–frequency distributions of simple-event beds show multimodal patterns, which oppose the sorting hypothesis and probably still reflect population dynamics. Some compositional bias is indicated by significantly lower proportions of right valves.

(3) Because single-event shell concentrations alternate with barren marlstones, background shell destruction rates during the deposition of marls were probably high. It is hypothesized that shell-rich tempestites of the Kössen Formation thus contain live bivalves or recently dead shells only. Shell-poor tempestites can generally reflect conditions when a sea-floor affected by storm contained no or sparsely distributed shelly populations.

(4) The upper parts of the siliciclastic intervals can be dominated by shell-poor tempestites and mostly contain rare shell concentrations, in contrast to the lower parts. This pattern indicates that either dead-shell production rates were lower or background shell destruction rates were higher in the shallower habitats in contrast to the deeper habitats.

(5) The differential body size patterns in shell concentrations were primarily driven by original between-habitat differences in bivalve body size. Small bivalve-dominated communities were typical of deeper habitats in contrast to large bivalve-dominated communities from shallower habitats.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2005.11.005.

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